University of Alberta

Ecological Interactions of Mountain Caribou, Wolves and Moose in the North Columbia Mountains, British Columbia

by

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Abstract

The Southern Mountain population of mountain caribou (*Rangifer tarandus caribou*) is threatened in Canada, with predation the proximate cause of these declines. To reduce predation risk, caribou isolate themselves from predators and other prey species. I examined the spatial partitioning of mountain caribou, moose (*Alces alces*), and wolves (*Canis lupus*), and mortality sources of caribou in the north Columbia Mountains, British Columbia (2003 – 2006). Spatial separation between caribou and wolves was highest in late winter and lowest in spring and calving season. Engelmann spruce/subalpine fir forests, alpine areas, and old forests (> 140 yrs) were important variables that separated these species. The main predator of adult caribou was bears, with wolf predation increasing in importance after 2000. Wolf diet was comprised of moose (91 – 99%) with small relative proportions of caribou, deer and beaver. This information will provide critical information for effective wildlife management and planning caribou recovery strategies.

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TABLE OF CONTENTS

Chapter 1: Introduction 1
1. Altered Predator-Prey Relationships 4
2. Thesis Overview 5
3. Literature Cited 8

Chapter 2: Mortality patterns and spatial partitioning among mountain caribou, moose, and wolves in the north Columbia Mountains, British Columbia. 12
1. Introduction 12
2. Study Area 17
3. Methods 19
   3.1. Animal captures 19
   3.2. Adult caribou mortality 20
   3.3. Modeling strategy 21
   3.4. GPS bias model 26
   3.5. Distance between species 27
4. Results 28
   4.1. Animal capture and telemetry data 28
   4.2. Adult caribou mortality 28
   4.3. Variables used to partition space 29
   4.4. Mapping Latent Selection Differences 32
   4.5. Distance between species 33
5. Discussion 34
   5.1. Adult caribou mortality 34
   5.2. Spatial and temporal separation 35
   5.3. Limitations and assumptions 43
6. Conclusions 43
7. Literature Cited 45

Chapter 3: Seasonal and pack variation in wolf diet using stable isotope analysis: implications for mountain caribou recovery 74
1. Introduction 74
2. Study Area 79
3. Methods 80
   3.1. Sample collection 80
   3.2. Diet composition 82
   3.3. Statistical analysis 87
   3.4. Extrapolating stable isotope relative proportions 87
4. Results 88
   4.1. Sample collection 88
   4.2. Isotopic signatures 89
   4.3. Diet composition 90
   4.4. Statistical analysis 91
   4.5. Extrapolating isotope relative proportions 91

5. Discussion 92
5.1. Average wolf pack diet 92
5.2. Wolf pack variation in diet 94
5.3. Seasonal variation 96
5.4. Extrapolating isotope relative proportions 98
5.5. Other considerations 99
6. Conclusions 100
7. Literature Cited 103

Chapter 4: Management Implications 120
1. Reducing predation 121
2. Managing habitat of primary prey 123
3. Literature Cited 125

LIST OF TABLES

Table 2-1. Description of variables used in RSF models to determine differences in habitat selection between mountain caribou, moose and wolves in five seasons in the north Columbia Mountains, British Columbia between 2003-2006 54

Table 2-2. The results from the likelihood ratio χ^2 tests and appropriate degrees of freedom for each seasonal model for each species comparison. All models were significant with p-values <0.01. 55

Table 2-3. The number of telemetry locations (GPS and VHF) per season from moose, caribou and wolves from the north Columbia Mountains, British Columbia between 2003 – 2006 (EW = early winter, LW = late winter, SP = spring, CA = calving, SU = summer). 55

Table 2-4. Coefficients and standard errors for the most parsimonious RSF model for differences in selection in five seasons between mountain caribou and wolves in the northern Columbia Mountains, British Columbia from 2003-2006. Coefficients in bold indicate significant variables in the models. Mountain caribou are coded as one and wolves are coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*). 56

Table 2-5. Coefficients and standard errors for the most parsimonious RSF model for differences in selection in five seasons between mountain caribou and moose in the northern Columbia Mountains, British Columbia from 2003-2006. Coefficients in bold indicate significant variables in the models. Mountain caribou are coded as one and moose are coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*). ... 57

Table 2-6. Coefficients and standard errors for the most parsimonious RSF model for differences in selection in five seasons between moose and wolves in the northern Columbia Mountains, British Columbia from 2003-2006. Coefficients in bold indicate significant variables in the models. Moose are coded as one and wolves are coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*). 58

Table 2-7. The Exp(β) of the most parsimonious RSF models used in the interpretation of the differences in selection in five seasons between mountain caribou, moose and wolves in the northern Columbia Mountains, British Columbia from 2003-2006 (EW = early winter, LW = late winter, SP = spring, CA = calving, SU = summer). Significant variables are highlighted in bold. The first species in the comparison heading is coded as one and the second is coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*). 59

Table 2-8. The degree of spatial separation (H = high, M = moderate, L = low) for three species comparisons in five seasons in the north Columbia Mountains, British Columbia. 60

Table 3-1. Summary of the means, standard deviations (SD) and ranges (min to max) for $\delta^{13}C$ and $\delta^{15}N$ values for hair of four potential prey species of wolves, sampled from the north Columbia Mountains, British Columbia from 2003-2005 (not corrected for consumer diet-hair fractionation). 110

Table 3-2. Summary of the means, standard deviations (SD) and ranges (min to max) for $\delta^{13}C$ and $\delta^{15}N$ values for hair of four wolf packs sampled from the north Columbia Mountains, British Columbia from 2003-2006. 110

Table 3-3. Initial multi-source mixing model results (Isosource) for the relative contribution and standard deviation of prey items wolf pack diets in the north Columbia Mountains, British Columbia from 2003-2006. 110

Table 3-4. Single-isotope and dual-isotope linear mixing model results (IsoError) for the percent and standard error of prey items wolf pack diets in the north Columbia Mountains, British Columbia from 2003-2006. Less common prey species were removed from the initial multi-source mixing model. 111

Table 3-5. Relative contribution and standard deviation of prey items to wolf diets for four time periods in the north Columbia Mountains, British Columbia from 2003-2006. Seasonal samples were extracted from the base (late fall) and tip (late spring) of wolf guard hairs (from Darimont and Reimchen 2002), and blood collected in March representing a 70 day time frame from Jan. 4 – March 15 (late winter). The mean year is a whole guard hair representing the diet from late spring to late fall (4-5 mo.; Darimont and Remchen 2002). 111

Table 3-6. Information used to calculate the relationship between percent caribou in diet and caribou density within each wolf pack home range in the north Columbia Mountains, British Columbia between 2003 - 2006. 112

LIST OF FIGURES

Figure 1-1. Outline of the study area encompassing the north Columbia Mountains, British Columbia, Canada. Mountain caribou subpopulations in the study area include Central Rockies, Columbia North, Columbia South and Frisbee/Queest (Wittmer et al. 2005). 7

Figure 2-1. Outline of the study area encompassing the north Columbia Mountains, British Columbia, Canada. Mountain caribou subpopulations in the study area include Central Rockies, Columbia North, Columbia South and Frisbee/Queest (Wittmer et al. 2005). 61

Figure 2-2. Mortality factors of adult radio-collared mountain caribou in the north Columbia Mountain study area, British Columbia from < 2000 (1992 - 1999) and > 2000 (2000 – 2006). Proportions were corrected for caribou sampling effort (number of caribou years) during each time period. The number above the bars indicated the raw number of mortalities within each mortality category. * Non-predation related unknown mortalities. MVA = motor vehicle accidents. Accident = natural disasters such as tree fall and rock crevasses. 62

Figure 2-3. Mortality factors of predation-related adult radio-collared mountain caribou in the north Columbia Mountain study area, British Columbia from < 2000 (1992 - 1999) and > 2000 (2000 – 2006). Proportions were corrected for caribou sampling effort (number of caribou years) during each time period. The number above the bars indicated the raw number of mortalities within each mortality category. 63

Figure 2-4. The proportion of telemetry locations for mountain caribou and moose falling within 1000 m buffers of wolves, and each other, for five seasons in the north Columbia mountains, British Columbia from 2003-2006. 64

Figure 2-5. Differences in resource selection between mountain caribou, wolves and moose in the early winter season from 2003-2006 in the north Columbia Mountains, British Columbia. 65

Figure 2-6. Differences in resource selection between mountain caribou, wolves and moose in the late winter season from 2003-2006 in the north Columbia Mountains, British Columbia. 66

Figure 2-7. Differences in resource selection between mountain caribou, wolves and moose in the spring season from 2003-2006 in the north Columbia Mountains, British Columbia. 67

Figure 2-8. Differences in resource selection between mountain caribou, wolves and moose in the calving season from 2003-2006 in the north Columbia Mountains, British Columbia..... 68

Figure 2-9. Differences in resource selection between mountain caribou, wolves and moose in the summer season from 2003-2006 in the north Columbia Mountains, British Columbia..... 69

Figure 2-10. The available and marginal use of forest age classes for caribou, moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006. 70

Figure 2-11. The available and marginal use of landcover for caribou, moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006. 71

Figure 2-12. The available and marginal use of distance to cutblock category for moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006. 72

Figure 2-13. The available and marginal use of distance to low-use road category for caribou, moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006..... 73

Figure 3-1. Outline of the study area encompassing the north Columbia Mountains, British Columbia. Included wolf home ranges (90% adaptive kernel volume) from VHF and GPS locations (2003-2006). The location of Mt. Revelstoke/Glacier Park home range was estimated (dashed line) for visual purposes only, because there were no collared individuals to accompany the stable isotope samples..... 113

Figure 3-2. Mountain caribou (2004 & 2006) and moose census data (2003) overlaid with wolf pack home ranges (90% adaptive kernel volume) from wolf VHF and GPS locations (2003-2006). The location of Mt. Revelstoke/Glacier Park wolf home range was estimated (dashed line) for visual purposes only, because there were no collared individuals to accompany the stable isotope samples..... 114

Figure 3-3. Distribution of mean $\delta^{13}C$ and $\delta^{15}N$ hair values (‰;±*SD*) for four main prey sources of wolves (■) and individual wolves (●). Wolves were sampled from five wolf packs in the north Columbia Mountains from 2003-2006. Prey sources were corrected for diet-hair fractionation (Roth and Hobson 2005)..... 115

Figure 3-4. Distribution of mean $\delta^{13}C$ and $\delta^{15}N$ hair values (‰; ±SD) for four prey sources (■), and five wolf packs (●) and sampled in the north Columbia Mountains from 2003-2006. Prey sources were corrected for diet-hair fractionation (Roth and Hobson 2005). 116

Figure 3-5. Mean values of $\delta^{13}C$ and $\delta^{15}N$ (± SD) for late spring ($n = 3$), late fall ($n = 2$), late winter ($n = 4$) and the year average ($n = 3$) for wolf packs sampled in the north Columbia Mountains from 2003-2006. Seasonal samples were extracted from the base (late fall) and tip (late spring) of wolf guard hairs (from Darimont and Reimchen 2002), and blood collected in March (late winter). The mean year is a whole guard hair collected in March that represented the diet from spring to fall. 117

Figure 3-6. Isosource mixing polygon for the mean $\delta^{13}C$ and $\delta^{15}N$ hair values (‰) for four prey species of wolf packs ($n = 4$) in the north Columbia Mountains, British Columbia from 2003 - 2006. I reported the 1^{st}-99^{th} percentile ranges for the calculated feasible distributions in Isosource..... 118

Figure 3-7. Isosource mixing polygon for the mean $\delta^{13}C$ and $\delta^{15}N$ a) late winter blood samples ($n = 4$), and b) mean year ($n = 3$), late spring ($n = 3$) and late fall ($n = 2$) hair samples for wolves in the north Columbia Mountains, British Columbia. The 1^{st}-99^{th} percentile ranges for the calculated feasible distributions are listed in Table 4. *n* represented the number of wolf packs sampled. 119

Chapter 1: Introduction

Interactions of animals in time and space are common themes in ecological studies (Sih 2005). Animals can respond to each other randomly, with attraction, or with avoidance, and these responses can be spatial, temporal, or a mixture of the two (Minta 1992). Predator-prey interactions are an example of both avoidance and attraction. Prey avoid predators while maximizing their energy intake (Lima and Dill 1990; Lima 1998; Sih 1992) while predators are attracted to prey . Predator avoidance can lead to reduced energy intake and have long-term effects on an animal's fitness (Lima 1998). Both immediate and long-term effects of predation may be reflected in an animal's use of space (e.g., choice of habitats; Lima 1998).

Optimal foraging theory predicts that individuals should maximize their net rate of energy intake subject to various constraints, resulting in the greatest fitness gain for the animal (Pyke et al. 1977; Krebs and Davies 1993; Caughley and Sinclair 1994). When both predators and prey are present, prey should avoid areas used by predators while ensuring adequate forage, and predators should concentrate their activity where prey are most dense (Lima 2002). Furthermore, if predators can select from more than one prey species, then the most profitable species should be selected based on the amount of energy gained, the time and effort expended in the search and handling of that prey item, and any risk (Royama 1970; Krebs and Davies 1993).

Prey can adopt antipredator strategies to reduce predation risk including physical traits, behaviour, and landscape use (Sih 1987; Mech and Peterson 2003).

For example, if a predator is less successful in a specific habitat type, then prey may select this habitat to reduce risk (Sih 2005). The use of refuges can have a stabilizing effect on predator-prey interactions (Rosenzweig and MacAurthur 1963). Differential use of space can cause a negative correlation between the spatial distributions of predators and prey (Sih 1984; Sih 2005). Therefore, the absence of prey from certain habitat types may reflect the effect of predators on broad-scale habitat use patterns (Lima 1998). The degree of spatial separation between predator and prey may be reflected in the associated level of predation experienced by the prey species. In North America, predatory-prey systems including caribou (*Rangifer tarandus*), moose (*Alces alces*) and wolves (*Canis lupus*) present an opportunity to examine such patterns.

Caribou-moose-wolf systems have been studied extensively to evaluate spatial separation between species (Seip 1992, James et al. 2004), predator-prey dynamics (Joly and Patterson 2003), wolf control programs (Boertje et al. 1996; Bergerud and Elliot 1998; Hayes et al. 2000, Hayes et al. 2003), and management options to recover caribou, a threatened species in Canada (Weclaw and Hudson 2004, Lessard et al. 2005). Here, I examine a caribou-moose-wolf system to evaluate spatial partitioning of resources, and the potential role of wolf predation on the decline of mountain caribou.

Mountain caribou are an ecotype of woodland caribou characterized by seasonal elevation migrations and dependence on arboreal lichen in winter. In 2000, the British Columbia (B.C.) government upgraded mountain caribou from a species of Special Concern (Blue List) to Endangered or Threatened (Red List;

B.C. Conservation Data Centre). This was followed, in 2002, by the national listing of the Southern Mountain Population as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The status of the Southern Mountain population was upgraded due to presence of generally small, isolated herds, declining populations, and threats within caribou ranges. A "Strategy for the Recovery of Mountain Caribou in British Columbia" (Mountain Caribou Technical Advisory Committee [MCTAC] 2002) provided direction for mountain caribou recovery based on best available science. The alteration of predator-prey relationships by industrial activities was one of the major threats identified in the document (MCTAC 2002). To address this threat, monitoring and management of predators and alternate prey species was recommended in mountain caribou habitat. A recent meta-analysis of mountain caribou populations in B.C. supported the hypothesis that predation was the primary cause of mountain caribou declines (Wittmer et al. 2005).

MCTAC (2002) identified the Revelstoke local mountain caribou population as high conservation priority, therefore the North Kootenay Recovery Action Group was established to develop a "regional" recovery plan. In 2004, an independent panel of scientists was commissioned to review the predator-prey-habitat interactions within the Revelstoke area and make recommendations to focus research priorities. This panel proposed a number of recommendations, including a 3 – 4 year wolf telemetry project to document territory and pack size, total population and the elevational/habitat use/overlap with caribou (Messier et al. 2004). Summer habitat use of moose was also identified as a research priority

(Messier et al. 2004). In response to these recommendations and scientific findings, local land managers, government agencies, and researchers initiated work to examine the impact of predators and alternate prey on the decline of mountain caribou in the north Columbia Mountains, B.C. (Figure 1-1). I began examining the ecological interactions of wolves, caribou and moose in 2003 as part of a larger, long-term research project with the Columbia Mountains Caribou Project (Revelstoke, B.C.).

1. Altered Predator-Prey Relationships

Predator-prey relationships may be altered by industrial activities, such as forest harvesting and road building. One of the outcomes of forest harvesting is the creation of early seral forest that provides a high quality food source for prey species such as moose (Peek 1998), thereby maintaining or increasing populations. For example, a 2003 moose census in the Revestoke region documented a 100% increase (0.7 moose/km^2 to 1.54 moose/ km^2) in moose densities over the past decade (Poole and Serrouya 2003). This increase was attributed to a higher proportion of young forest on the landscape, and milder winters that enhance overwinter survival (Serrouya and D'Eon 2003). Increases in moose densities may have resulted in a corresponding increase of wolves on the landscape (Messier 1994). Such changes in species composition and abundance may exacerbate population declines and extinction of mountain caribou by "apparent competition" (Holt 1977; Holt and Lawton 1994; Wittmer et al. 2007). Apparent competition occurs when two noninteracting prey species

negatively affect each other by altering the density or foraging behaviour of a common predator (Holt 1977; Holt and Lawton 1994). To reduce the negative effect of increased predation, woodland caribou isolate themselves from predators and other more abundant prey species (Bergerud and Page 1987; Seip 1992; James 1999; McLoughlin et al. 2005). Bergerud et al. (1984) suggest that the dispersion tactic adopted by woodland caribou is no longer sufficient to reduce predation because recent predator increases have increased the number of predators searching per unit area, resulting in higher mortality rates of caribou. Researchers also suggest that loss of mature forests (Wittmer et al. 2005) and fragmentation of caribou winter range (Smith et al. 2000) may also be compromising the 'spacing away' antipredator strategy used by caribou. Comparison of resource selection by wolves, caribou and moose, and the diet analysis of wolves can be used to evaluate and refine these hypotheses.

2. Thesis Overview

The main goal of my research was to provide information for the effective recovery of mountain caribou by contributing to enhanced understanding of predation by wolves and management of habitat for prey (caribou and moose). I addressed the following management questions: (1) do landscape conditions contribute to spatial separation of caribou, wolves and moose; (2) do these relationships vary seasonally, and (3) should wolves be the focus of predator management efforts in the north Columbia Mountains, B.C.?

The substantive data chapters of this thesis are written in manuscript format, therefore there is some overlap in the introduction, study area and methods sections between chapters. In Chapter 2, I examine the spatial partitioning of resources between mountain caribou, moose, and wolves in the Revelstoke area between 2003 - 2006. I quantify these relationships using Latent Selection Difference Functions (LSDF; Czetwertynski et al. In Prep) to directly compare the resource selection of caribou and wolves, caribou and moose, and moose and wolves over five seasons. My objectives were to determine if spatial separation was occurring, whether this changes between seasons, and what factors are important in separating these species. In this chapter, I also examine mortality sources for mountain caribou from 1992 - 2006 to determine if current levels of spatial separation are reflected in predation patterns. In Chapter 3, I examine stable carbon and nitrogen isotope ratios in the hair and whole blood of grey wolves from 2003 – 2006 to determine the relative importance of caribou and moose in the diet of wolves. I describe average wolf pack diet and how this varies by wolf pack and season (late spring, late fall, late winter). I also combine data from the literature and stable isotope results to estimate the actual amount of caribou in wolf diets. Chapter 4 outlines the potential management implications of my research in the broader context of caribou recovery efforts.

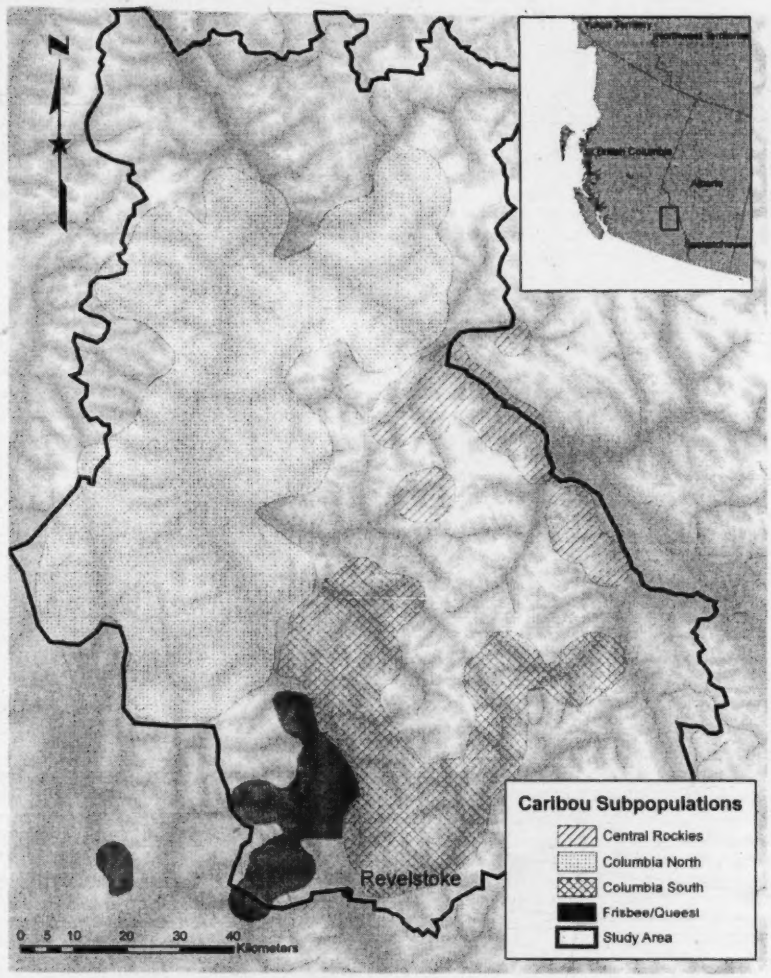

Figure 1-1. Outline of the study area encompassing the north Columbia Mountains, British Columbia, Canada. Mountain caribou subpopulations in the study area include Central Rockies, Columbia North, Columbia South and Frisbee/Queest (Wittmer et al. 2005).

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Chapter 2: Mortality patterns and spatial partitioning among mountain caribou, moose, and wolves in the north Columbia Mountains, British Columbia.

1. Introduction

Caribou *(Rangifer tarandus)* are a species of deer (Cervidae) that live in the tundra, taiga and montane forests of northern Europe, Asia and North America. In Canada there are four subspecies of caribou, including woodland (*R. tarandus caribou*), Peary (*R. tarandus pearyi*), Grant's (*R. tarandus granti*) and barrenground caribou (*R. tarandus groenlandicus*). Differences between subspecies are based not only on geographic location, topography and climate (Thomas and Gray 2002) but differences in behaviour, genetics and morphological features. For example, barrenground and woodland caribou differ in their average herd size, migrational patterns, body size and winter feeding habitats. Woodland caribou are further divided into five populations or ecotypes (Northern and Southern Mountain, boreal, Atlantic and Newfoundland; Thomas and Gray 2002). The Southern Mountain population, the focus of this research, lives primarily in the high-snowfall regions of southeastern British Columbia, and is characterized by distinct elevational migrations and dependency on arboreal lichen in the winter (Mountain Caribou Technical Advisory Committee 2002).

Moose (*Alces alces*) also belong to the Cervidae family and live in boreal and mixed deciduous forests of Canada and northern parts of America, Europe and Asia. In North America, moose and woodland caribou are sympatric over

most of their current geographical range (Boer 1998). Nevertheless, the coexistence of moose and caribou is a relatively recent event in central and southern British Columbia (B.C.), although historical records cite scattered moose populations in the Southern Interior Mountains (Spalding 1989). Population increases of moose in this region occurred subsequent to a significant natural range expansion in the 1900's, when human alteration of habitat, and climatic warming, created favorable conditions (Kelsall and Telfer 1974; Tefler 1984; Spalding 1989; Karns 1998). Common predators of woodland caribou and moose are wolves (*Canis lupus*), grizzly bears (*Ursus arctos),* black bears (*Ursus americanus*) and cougars (*Felis concolor*; e.g. Bergerud et al. 1984; Seip 1992; Flaa and McLellan 2000; Kinley and Apps 2001; James et al. 2004; Wittmer et al. 2005). Declines of woodland caribou populations (e.g. northern B.C., Bergerud and Elliot 1986) have been linked to the expansion of moose and the subsequent increase of wolves and associated predation across caribou distribution. To reduce predation, woodland caribou isolate themselves from predators and other more abundant prey species (Bergerud 1983; Bergerud and Page 1987; Seip 1992; McLoughlin et al. 2005). Bergerud et al. (1984) suggest that the dispersion tactic adopted by woodland caribou is no longer sufficient to reduce predation because recent predator increases have increased the number of predators searching per unit area resulting in higher mortality rates of caribou. Researchers also suggest that loss of mature forests (Wittmer et al. 2005) and fragmentation of caribou winter range (Smith et al. 2000) may be compromising the 'spacing out' antipredator strategy used by caribou, by altering the density and distribution of

alternate prey populations, and resultant patterns of habitat use by predators. Road networks associated with loss of mature forests and fragmentation may also increase the efficiency of movement and access of predators into previously roadless areas inhabited by caribou.

The risk of predation is affected by patterns of habitat selection (McLoughlin 2005) because habitats and landscape attributes render prey more or less susceptible to predation (Hebblewhite et al. 2005). For example, woodland caribou in Alberta experience higher than expected levels of predation risk in upland areas and reduced predation risk by selecting peatland habitats (McLoughlin 2005). In mountainous areas, caribou show distinct seasonal elevation shifts to take advantage of food availability, and/or avoid predation (Bergerud et al. 1984; Seip 1992; Apps et al. 2001), creating seasonal variation in their pattern of spatial separation from moose and wolves. Mountain caribou within my study area prefer old western red cedar (*Thuja plicata)*, and western hemlock (*Tsuga heterophylla*) forests at lower elevations in early winter (Apps et al. 2001). In late winter, when snow is deep and consolidated enough to access arboreal hair lichen in the canopy of standing trees, they move to forests at higher elevations dominated by subalpine fir (Simpson et al. 1987; Apps et al. 2001). In spring, they descend to low elevation cedar and hemlock forests, and in summer shift to higher elevations of old Englemann spruce (*Picea Engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests to access forbs and deciduous vegetation (Simpson et al. 1987; Rominger et al. 2000; Apps et al. 2001).

Seasonal habitat preferences of moose differ from those of mountain caribou. Moose living in mountainous areas in North America select open, upland (stream valley shrub, alluvial) and aquatic habitats in the spring (Tefler 1984; Peek 1998). These habitats provide high quality abundant forage and protection against heat (Peek 1998). In summer and fall, moose migrate to higher elevations to subalpine forests, and shrublands above the timberline to take advantage of wet meadow complexes (Tefler 1984). In the early winter, moose move to open areas with high biomass of low shrubs (Peek 1998; Tefler 1984). In western interior montane forests of B.C., moose move downhill in the late winter to gentler slopes with higher solar insolation to take advantage of high forage habitats and lower snow depths (Poole and Stuart-Smith 2006). Moose avoid alpine areas in all seasons (Boer 1998). As a predator of both moose and caribou, wolf resource selection at the landscape scale may be best predicted by prey availability. However, prey abundance does not necessarily translate to prey availability as hunting success may be influenced by features like snow depth and elevation in mountainous regions (e.g. Minnesota, Fuller 1991, Rocky Mountains, Callaghan 2001).

This study examines caribou mortality sources and the spatial relationships between mountain caribou, moose, and wolves in the north Columbia Mountains, B.C., between 2003 and 2006. Wolves are major predators of adult mountain caribou in northern (Bergerud et al. 1984), and central B.C. (Seip 1992), with cougars being the main predator of caribou in southeastern, B.C. (Kinley and Apps 2001). Previous studies in various regions have described

patterns of resource selection between moose, caribou, and wolves, but have not quantified the strength of these differences (Bergerud et al. 1984; Bergerud and Page 1987; Seip 1992; Cumming et al. 1996; James et al. 2004; Neufeld 2006). I quantify differences in habitat selection of caribou, moose, and wolves, as well as identify caribou mortality factors, in order to provide critical information for caribou recovery strategies and landscape management of caribou habitat. This information is also important to determine the role of wolves in structuring habitat use patterns of caribou, and the effectiveness of caribou antipredator tactics at reducing wolf predation. My specific objectives were to: (1) identify mortality factors affecting adult caribou, (2) determine if spatial separation is occurring between moose, caribou, and wolves, (3) explore how this relationship changes between seasons, and (4) identify what terrain, habitat, and human-use factors are important in separating these species.

2. Study Area

The study area (~9,000 km^2) was located in the Northern Columbia Mountain ecoregion in southeastern B.C. (51°N 118°W; Figure 2-1; Demarchi 1996). Rugged, mountainous terrain (550 m to 3,050 m) and high precipitation levels (946 mm/yr, 425 cm falling as snow) characterize the area. The landscape was a mosaic of forests, regenerating clear-cuts, riparian area, shrublands, upper elevation basins, and avalanche chutes. Biogeoclimatic subzones range from Interior Cedar-Hemlock (ICH) in the valley bottoms and mid-elevations, to Engelmann Spruce-Subalpine Fir (ESSF) at approximately 1,280 m to 1,400 m (Braumandl and Curran 1992). The Alpine Tundra subzone occurs at elevations above the ESSF.

Western red cedar, and western hemlock dominate the ICH subzones whereas Douglas-fir (*Pseudotsuga menziesii*) is less common (Braumandl and Curran 1992). The ESSF zone comprises coniferous forests of primarily Englemann Spruce and subalpine fir (Braumandl and Curran 1992). Alpine meadows, shrublands, snowfields, glaciers and rock dominate the Alpine Tundra zone. Two hydroelectric developments in 1973 and 1984 flooded most of the low elevation riparian habitat and significantly altered the study area (BC Hydro 2007). Forest harvesting and silviculture, hunting, trapping, snowmobiling and heliskiing were the major human-use activities in the region during the research period.

Moose was the most abundant and widespread ungulate in the region, however low densities of mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*) and elk (*Cervus canadensis*) occurred in the southern portion of the study area (Poole and Serrouya 2003). Mountain goats (*Oreamnos americanus)* also inhabited the more mountainous portions of the study area. Mountain caribou existed at low densities and were delineated into four subpopulations (Figure 2-1; Columbia North, Columbia South, Frisby/Queest and Central Rockies; Wittmer et al. 2005). Grizzly bears, black bears, wolverine (*Gulo gulo*), wolves, and cougars occurred throughout the area. Information on predator densities was not available at the time of this study.

In 2000, mountain caribou subpopulations within the study area were Red Listed in British Columbia (Conservation Data Centre; Mountain Caribou Technical Advisory Committee 2002) and listed nationally as Threatened in 2002 (Committee on the Status of Endangered Wildlife in Canada). Since 1997, these subpopulations have experienced an annual decline of 10% after a relatively stable period between 1994 to 1997 (McLellan et al. 2006). Current caribou densities within the four subpopulations range from 0.035 – 0.05 caribou km^{-2} (Wittmer et al. 2005). In contrast, moose densities in the region doubled in the past decade (1993 – 2003) from 0.7 moose km^{-2} to 1.54 moose km^{-2} (Poole and Serrouya 2003). This increase coincided with increases in the proportion of younger forests resulting from regeneration subsequent to forest harvesting. Large-scale forestry began in the 1960's and focused on harvesting of older age

forests. Currently, 60% of merchantable forests is less than 30 years old and 40% is over 200 years old (R. Serrouya, pers. comm.)

3. Methods

3.1. Animal captures

Wolves, moose, and mountain caribou were captured from 2002 to 2006 by net-gunning from a helicopter (Bighorn Helicopters Inc., Cranbrook, B.C). I equipped animals with Global Positioning System (GPS) or Very High Frequency (VHF) radio-collars (Advanced Telemetry Systems, Insanti, Minnesota, USA; Lotek Inc.,Newmarket, Ontario, Canada; Telonics, Inc., Mesa, Arizona, USA; HABIT, Victoria, B.C., Canada; University of Alberta Protocol 2004-09D, 2005-19D and Parks Canada). Fourteen wolves from four packs (March 2004 and 2005) were captured and equipped with six GPS (Lotek GPS_3300s; HABIT) and eight VHF (Lotek LMRT_3) radio-collars. Twenty-six moose were captured in March 2004 and 2005 and affixed with 13 GPS and 13 VHF radio-collars. Thirty-seven mountain caribou were collared from March 2001 – March 2006 and affixed with 10 GPS and 27 VHF collars. Only data from 2003 – 2005 were used from these caribou. The GPS fix schedules were species specific (wolves every four hours, moose every five hours, mountain caribou every two - six hours).

I used Apps et al. (2001) definition of five caribou seasons using the average date of the greatest seasonal elevation shift made by collared caribou in the study area. These seasons were defined as: early winter (Oct. 23 – Jan. 15), late winter (Jan. 16 – Mar. 31), spring (Apr.1 – May 23), calving (May 24 – June

15), and summer (June 16 – Oct. 22). I divided moose and caribou locations into these five seasons. I divided wolf locations into summer (April 1 – Oct. 22) and winter (Oct. 23 – Mar. 31) only, because of lower sample sizes. I compared "summer" wolf locations to spring, calving and summer caribou and moose locations. I compared wolf "winter" locations to caribou and moose early and late winter locations.

3.2. Adult caribou mortality

All radio-collared caribou were located bi-weekly from a fixed-wing aircraft and monitored for mortalities. Sensors in the radio-collars also registered mortalities by altering their beacon frequency when a collar was immobile for more than six hours. Field crews investigated an animal mortality by ground as soon as possible to determine the cause of death. The cause of death was identified as a predation event if there was blood, subcutaneous hemorrhaging at wound sites, or signs of a struggle (Kunkel et al. 1999). The species of predator was identified based on carcass use, scat, tracks and hair around the kill site.

To increase samples sizes, I used additional caribou mortality data from a long-term study (1992 – 2006) in the same study area. These data, prepared by the Columbia Mountains Caribou Project (Revelstoke, B.C.), were divided into pre-2000 and post-2000 to reflect changing predator-prey dynamics over the 14 year time period. The year 2000 was selected as the separating point between time periods, because moose populations were increasing at the greatest rate during this year, peaking in 2003 (Serrouya, pers. comm.). The data were corrected for sampling effort by dividing the raw number of deaths attributed to

each mortality factor by the number of "caribou years". A "caribou year" is the sum of the number of caribou monitored, multiplied by the number of years each caribou was monitored (until the collar fell off, battery died, or animal died).

3.3. Modeling strategy

3.3.1. Variable selection

I selected terrain, habitat, and human-use variables to quantify the difference in habitat selection between moose, caribou, and wolves. I used dummy coding for all categorical variables in the analysis (Stata Corp. 2006).

I extracted terrain variables such as elevation, slope, aspect, and terrain ruggedness index (TRI) from 1:50,000 digital elevation maps (DEM) and classified aspect as a binomial categorical variable (south or north). North aspect was coded as the reference category. I used equations modified from Nellemann and Cameron (1996) and the relative richness index of Turner (1989) to calculate a terrain ruggedness index. This calculation used slope and aspect data derived from a 30 m DEM according to the following formula:

equ 1

$$TRI = \frac{(\text{aspect variation} \times \text{average slope}) / (\text{aspect variation} + \text{average slope})}{100}$$

where aspect variation measures the number of aspect classes in a 300 m moving circular window over the maximum number of aspect classes in the study

area.

I derived habitat variables that included landcover (5 classes), forest age (4 classes), and crown closure from the British Columbia Ministry of Forests (MOF) inventory database at a 30 m x 30 m resolution (Table 2-1). Reference categories were designated as cedar/hemlock for landcover and 41-100 yrs for forest age. I used a coarser resolution (300 m x 300 m) for habitat variables on private land because finer resolution information was not available.

I represented human-use variables as distance to cutblock and distance to low-use road (gravel, trail, powerline; e.g. Whittington et al. 2005). Distance to high-use paved roads was not included in the analysis because it was highly correlated to other variables. I split distance to cutblock into four distance categories (reference category = 501-2000 m; Table 2-1) to represent distances that may influence resource selection by animals. I acquired road and cutblock information from forest licensees in the study area (Revelstoke Community Forest Corporation, Downie Street Sawmills Ltd.) and coverages from the National Topographic Data Base (Geomatics Canada). For areas without digital forest coverage (private land), I digitized cutblocks from ortho-photos and merged them to create a seamless map of cutblocks. I used four categories to evaluate the effect of roads on animal resource selection (reference category = 501-2000 m; Table 2-1; e.g. James and Stuart-Smith 2000; Oberg 2001; Dyer et al. 2002; Whittington et al. 2005). I resampled GIS layers at a 100 m x 100 m pixel size to account for average location error of GPS and VHF location data. I selected a 100 m pixel size because previous research in mountainous terrain estimates that

95% of location error is <113 m for GPS collars and < 200 m for VHF collars (Hebblewhite 2006). I used ARCMAP 9.1 (Environmental Systems Research Institute, Redlands, CA, USA) and Hawth's Analysis Tools Version 3.21. for all GIS analyses.

3.3.2. Comparing resource selection

I used a Latent Selection Difference Function (LSD; Czetwertynski et al. In Prep) to directly compare the resource selection of caribou and wolves, caribou and moose, and moose and wolves over five seasons. I assumed that resources were equally available to all species and applied this method to quantitatively compare groups at the landscape scale (Czetwertynski et al. In Prep). I used logistic regression to estimate coefficients (Czetwertynski et al. In Prep; Manly 1993); for example, coding caribou locations as (1) and wolf locations as (0), thereby eliminating the use of availability in the equation. The selection of what habitats are available to an animal can significantly affect the analysis in use-availability designs, and may result in misleading conclusions affected by sampling protocol (Keating and Cherry 2004) and the scale of investigation (Johnson 1980). This method allows for direct comparisons of habitat selection and results in meaningful measurements of strength of relationships. The relationship has the following log-linear form:

eqn 2

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i)$$

where w(x) represents the resource selection of one species compared to another and β_i are the coefficients estimated for environmental predictors x_i (Manly 1993).

Variable reduction was achieved by subjecting the full set of variables to a number of criteria to establish the final model set. Variables had to satisfy the following criteria: biologically relevant, ecologically plausible, uncorrelated, significant in univariate modeling (Graf et al. 2005), consistent algebraic sign in both univariate and multivariate models, and satisfy the assumptions of logistic regression (Hosmer and Lemeshow 2000). If two variables were correlated ($r > |0.7|$; Tabachnick and Fidell 1996), I retained the variable with the lowest log-likelihood value and the smallest p-value (Boyce et al. 2002). I omitted variables with low predictive power in univariate models (Walds Chi^2, $p > 0.25$), and used Box Tidwell regression models to detect nonlinearity in the logit. I removed elevation as a variable in the analysis because, although highly predictive, it was correlated with other variables that were more amenable to manipulation by resource managers (e.g. landcover, distance to low-use road). Because of nonlinearity, I categorized the variables forest age, distance to cutblock, and distance to low-use road. Due to the exploratory nature of this analysis, I used a stepwise regression algorithm to select variables, with cut-off values of 0.05 (P enter) and 0.10 (P remove; Montgomery and Peck 2001). I used the robust cluster option and the Huber/White/sandwich estimator of variance (Stata Corp 2003) in the logistic regression model to account for bias and temporal autocorrelation (Boyce et al. 2002; Thomas and Taylor 2006). I validated the models using *k*-fold

cross-validation procedures (Fielding and Bell 1997). A Spearman's-rank correlation (rho) of > 0.64 is considered significant and indicates that the model has good predictive ability (Boyce et al. 2002).

3.3.3. Model interpretation

The model results represent the resource selection of the species coded as 1 compared to the resource selection of the species coded as 0 (Czetwertynski et al. In Prep). For example, in the caribou and wolf comparison, the resource selection of caribou was always compared to wolf resource selection. The sign and magnitude of the β coefficients indicate the degree by which the two species differ in their resource selection (Czetwertynski et al. In Prep). If there is no difference in resource selection between the two species, then the coefficients are close to zero or non-significant. Negative or positive signs indicate avoidance or preference of a resource by the species coded as 1 compared to the reference species coded as 0. The coefficient of a continuous variable is defined as the percent change in probability of use by one species, compared to the reference species, with every unit change of the variable, while holding all other covariates constant. The coefficient of a categorical variable is the number of times the probability of one species use increases or decreases in that category, compared to the other species resource selection (Czetwertynski et al. In Prep).

I overlaid model coefficients on GIS maps to visually distinguish areas where selection varied between species. There are no species interactions implied by these maps, but only where one species is more likely to occur than the other.

3.4. GPS bias model

Fix-rate bias is defined as the probability of a radiocollar acquiring a GPS fix, given terrain and habitat features (D'Eon et al. 2002). Poor GPS fix rates can bias models, influencing the assessment of resource selection by animals (Frair et al. 2004). I developed a GPS bias model to correct for fix-rate bias, based on the methods of Frair et al. (2004) and D'Eon et al. (2002). I applied the GPS bias model developed by D'Eon et al. (2002) to my study area. The probability of acquiring a fix (P_{ACQ}) was calculated using;

equ 3

$$P_{ACQ} = 0.098 \text{ x available sky} - 0.076 \text{ x canopy cover} + 95.363$$

D'Eon et al. (2002) defined the variable "available sky" (AS) as the proportion of sky available to a GPS collar through direct line of sight in all directions and at all angles without terrain obstructions (disregarding forest cover). Due to the large size of my study area and limitations in computer processing ability, I modified the calculation of AS. With assistance from the Spatial Information Systems Laboratory (University of Alberta, Edmonton, Alberta), I used a DEM (100 m x 100 m) to represent the ground, and a matrix of points (sky matrix) with a 300 m x 300 m spacing to represent the sky. The sky matrix was set at 100 metres above the highest point in the landscape. Using the VISIBILITY function within ARCMAP GIS (Environmental Systems Research Institute, Redlands, CA), I calculated the proportion of the total number of sky matrix points visible from each location on the ground. Canopy cover (%) was

derived from MOF inventory database for the study area. The canopy cover data for private land was represented at a 300 m x 300 m resolution because finer resolution information was not available for those areas. I weighted each GPS telemetry location by the inverse probability of having acquired that location (P_{ACQ}), in essence "replacing" missing locations (Frair et al. 2004).

3.5. Distance between species

Spatial separation between species can be illustrated, not only by examining differences in resource selection, but proximity between species. Past studies have used distance to nearest neighbour measurements of track densities (Cumming et al. 1996) and distance to travel routes of predators (Bergerud and Page 1987) to elucidate spatial relationships between predators and prey. To gain a more thorough understanding of how moose, caribou, and wolves spatially separated themselves on the landscape, I measured the distance between species telemetry locations. I created multiple circular buffer rings of 1000 m each, to a maximum distance of 5000 m, around each wolf and caribou telemetry point for each season. I randomly selected 1000 m for each buffer distance. I used multiple buffer rings (1000 m – 5000 m), instead of one distance, to represent the possible range that wolves may be able to detect moose or caribou. Wolves locate prey by tracking, scenting or by sight (Peterson and Cuicci 2003). Wolves are reported to detect moose at distances ranging from 274 m to 2.4 km (Peterson and Cuicci 2003).

I calculated the proportion of caribou and moose telemetry points for each season within each wolf buffer to elucidate patterns of spatial separation. For the

moose and caribou comparison, I calculated the proportion of moose locations within each caribou buffer for each season.

4. Results

4.1. Animal capture and telemetry data

Of the 14 wolf collars deployed, all six wolf GPS collars failed prematurely, however, both Lotek_3300s collars were located and retrieved. I used data from 22 collared-moose, (five GPS and 17 VHF) and 35 mountain caribou (10 GPS and 25 VHF). Animals with less than 15 locations, or that fell outside of the designated study area were not used in the analysis. I used both GPS and VHF (100 m) locations to increase sample sizes. The average fix-rates for GPS collars deployed on mountain caribou (50%), wolves (45%), and moose (67%) were below the 80% value deemed appropriate for RSF analyses (Friar et al. 2004), therefore I applied the GPS bias model. Steep, mountainous terrain, dense forest cover and collar malfunction may have attributed to these low GPS fix-rates.

The average number of locations per season was 2027 (*SD* = 884.7), 1237 (*SD* = 669.8), and 699 (*SD* = 359.8) for caribou, moose and wolves respectively (Table 2-3). I pooled data for each species from Jan. 1, 2003 to March 31, 2006 and assumed that differences between years and wolf packs were negligible.

4.2. Adult caribou mortality

There were 117 collars distributed between four caribou subpopulations in the study area during 1992 – 2006. Sampling effort in the post-2000 time period

(110.5 caribou years) was approximately half that compared to pre-2000 (197.2 caribou years). There were 51 adult radio-collared mountain caribou mortalities recorded, with predation being the number one source of adult caribou mortality in both time periods (Figure 2-2). The proportion of predation-related deaths increased by 28% after 2000 (Figure 2-2), due to increases in grizzly, cougar and wolf predation. Grizzly and black bear predation was the major cause of adult caribou mortality before and after 2000 (Figure 2-3). Wolf predation increased from 0% to 21% after 2000 (Figure 2-3). Approximately 19% and 11% of mortalities were classified as unknown in < 2000 and >2000 respectively, but are suspected to be predation-related.

4.3. Variables used to partition space

Although a number of factors were important in discerning space selected by different species, I here address the three variables with the highest coefficients (Exp(β)) to discuss in detail (Table 2-7), and refer to the marginal habitat use graphs (Figure 2-10 – Figure 2-13) to aid interpretation.

4.3.1. Caribou and wolves

Mountain caribou and wolves partitioned space by differential use of old forests, spruce/subalpine fir and alpine, in the early winter (Table 2-4 & Table 2-7). Compared to a reference category (cedar/hemlock forests), mountain caribou were 24.3 times more likely to select older forests and 6.3 times more likely to select spruce/subalpine fir than wolves in the early winter (Table 2-4 & Table 2-7). Similarly, mountain caribou were 85.6 times more likely to select alpine areas

than wolves in the early winter relative to cedar/hemlock forests (Table 2-4 & Table 2-2-7). This level of interpretation can be applied to all variables in the analysis (see Table 2-7).

In the late winter, old forests, alpine, and areas within 100 m of roads were variables that mountain caribou and wolves used in different proportions (Table 2-4 & Table 2-7). The strength of these differences increased compared to early winter values (Table 2-7). Mountain caribou and wolves partitioned space in the spring by differentially selecting areas that were greater than 2000 m from a road, within 100 m of a road, and in the alpine (Table 2-4 & Table 2-7). Mountain caribou and wolves partitioned space in the calving season first by distances within 100 m of a road, then by alpine areas, followed by terrain ruggedness (Table 2-4 & Table 2-7). Mountain caribou and wolves used the following variables in different proportions on the landscape in the summer; distances from 0 – 500 m from a road, and alpine areas (Table 2-4 & Table 2-7). All caribou and wolf models were significant (Table 2-2) and had good predictive capability based on Spearman's-rank correlation from *k*-fold cross validation procedure (Table 2-4).

4.3.2. Caribou and moose

The spatial separation of mountain caribou and moose was indicated by their dissimilar use of areas between 100 – 500 m, and greater than 2 km from roads, as well as their use of alpine in the early winter (Table 2-5 & Table 2-7). In the late winter, mountain caribou and moose partitioned space first by their use of distances greater than 2000 m from roads, then by their use of alpine, followed

by 100 – 500 m from roads (Table 2-5& Table 2-7). Similar to the late winter season, mountain caribou and moose used areas greater than 2000 m and within 100 – 500 m from roads, and alpine areas differently in the spring (Table 2-5 & Table 2-7). Caribou selection of areas greater than 2000 m from a road was 1510 times more than that of moose. The three most influential variables separating mountain caribou and moose during calving were distances greater than 2000 m from roads, alpine, and old forests (Table 2-5 & Table 2-7). Mountain caribou and moose partitioned space based on distances greater than 2000 m and between 100 – 500 m from roads, and ruggedness of terrain in the summer (Table 2-5 & Table 2-7). All caribou and moose seasonal models were significant, (Table 2-2) and had good predictive ability based on *k*-fold cross validation results (Table 2-5).

4.3.3. Moose and wolves

Moose and wolves partitioned space by their differential use of areas 0 – 500 m from cutblocks (Table 2-6 & Table 2-7). Although distances >2000 m from a cutblock were significant in the model, moose and wolves used this category <5%, therefore I did not consider the variable biologically significant (Figure 2-12). Moose and wolves selected areas 0 – 100 m and 100 – 500 m from roads, as well as forests of less common species (deciduous, pine, Douglas fir) in different proportions in the late winter (Table 2-6 & Table 2-7). The forest-other category composed <10% of the landscape, although moose and wolves selected this category close to available proportions (Figure 2-11). Moose and wolves differentially selected areas within 100 m and 500 m of cutblocks and old forests

(141-680 yrs) in the spring (Table 2-6 & Table 2-7). Alpine habitat and areas greater than 2000 m from a cutblock were significant, but disregarded because moose and wolves used these variables <5% (Figure 2-11 & Figure 2-12). Moose used distances between 0 – 100 m from a cutblock, forests dominated by spruce/subalpine fir, and non-forested landcover types in different proportions than wolves during the calving season (Table 2-6 & Table 2-7). Both moose and wolves had similar selection for proximity to cutblocks in the summer, with exception of significant avoidance of distances between 100 – 500 m by moose compared to wolves (Table 2-6 & Table 2-7). All moose and wolf seasonal models were significant (Table 2-2), but the predictive capability varied seasonally based on *k*-fold cross validation results (Table 2-7). The predictive abilities of the models ranged from very good in the early winter, moderate in the spring, calving and summer, to poor in the late winter.

4.4. Mapping Latent Selection Differences

Figure 2-5 – Figure 2-9 indicated differences in relative resource selection between species in each comparison. For example, green areas in the caribou and wolf comparison (Figure 2-6a), suggest a greater likelihood of encountering a caribou than a wolf, whereas in red areas, wolf encounters are more likely.

In the early and late winter, the likelihood of encountering a caribou was low across the study area compared to wolves. LSDF models produced maps with few, small, isolated, high elevation patches where caribou were more likely to occur than wolves (Figure 2-5a & Figure 2-6a). In snow-free seasons (spring, calving, summer) the likelihood of encountering a caribou (compared to wolves)

was highest in areas above valley bottoms, away from areas characterized by low-use roads and cutblocks (Figure 2-7a – 2-9a).

Similar to the caribou and wolf comparison, LSDF models produced patterns of small, isolated, high elevation patches where caribou were more likely to occur than moose, although the size, and distribution of these areas increased in snow-free seasons (Figure2-5b & Figure 2-9b).

In general, LSDF maps produce patterns that showed that areas where moose were more likely to occur than wolves shifted from valley bottoms near cutblocks in the early winter, to areas situated away from cutblocks in the mid-high elevations in the summer (Figure 2-5c – Figure 2-9c). Moose had limited areas where they were more likely to occur relative to wolves in the spring (Figure 2-7c).

4.5. Distance between species

The proportion of mountain caribou locations within wolf buffers differed by season, with spring and late winter representing the highest and lowest proportions respectively (Figure 2-4a). Overall, there was a very small proportion of caribou locations within 1000 m of wolves during all seasons (Figure 2-4a). Spring and summer represented seasons when moose had the highest proportion of locations in mountain caribou buffers, up to distances of 3000 m when proportions declined in all seasons (Figure 2-4b). The proportion of moose locations 1000 – 5000 m from wolves was high in all seasons except summer (Figure 2-4c). The proportion of moose declined by approximately 23% within 0 – 1000 m from wolf locations in all seasons (Figure 2-4c).

5. Discussion

I quantitatively measured the differences in resource selection among three species to provide insights into the degree of spatial separation, factors that contribute to spatial separation, and how spatial separation varies seasonally. I also examined mortality factors of adult radio-collared caribou to determine the extent to which wolves contribute to adult caribou mortality.

5.1. Adult caribou mortality

The main predators of adult mountain caribou in the north Columbia Mountains, B.C., between 1992 - 2006 were bears (grizzly and black), with wolf predation increasing in importance after 2000. A recent meta-analysis of caribou subpopulations in B.C., found that bear predation occurs at approximately equal rates across mountain caribou distributions (Wittmer 2004). Grizzly and black bears are also found to be important predators of caribou neonates (e.g. Adams et al. 1995b; Rettie and Messier 1998), usually within the first 10 days after the onset of calving. Conversely, wolves did not appear to be a major cause of early calf mortality in areas directly west of the study area (Seip 1992). In northern British Columbia, wolves contributed to 30% (five mortalities) of calf mortalities occurring after calves were 18 days of age (Gustine et al. 2006). Wittmer et al. (2005) found that adult caribou were more likely to die due to predation during calving and summer than other seasons. My results and previous research suggest that the main predators of adult caribou vary geographically in B.C., from wolves in Quesnel Lake (Seip 1992), bears (grizzly and black) in the northern Columbia

Mountains and cougar in the Southern Purcell Mountains (Kinley and Apps 2001). However, the increase in wolf predation in the north Columbia Mountains since 2000 suggests that wolves may be a concern for caribou conservation because wolves have the capacity to respond numerically to increases in moose densities (Messier 1994; Messier and Joly 2000). Thus, if current trends in moose densities continue, wolves may pose a future threat to mountain caribou persistence (i.e. apparent competition; Holt and Lawton 1994; Messier 1994; Messier et al. 2004). Nevertheless, environmental (snow depth), behavioural (intraspecific competition), antipredator tactics (spatial refuge) and anthropogenic factors (hunting) may inhibit the ability of wolves to respond numerically to moose densities (Mech and Peterson 2003).

5.2. Spatial and temporal separation

My analysis indicated that mountain caribou, wolves and moose experienced different levels of spatial separation and this varied by season. I designated the degree of spatial separation as high, medium or low (Table 2-8), depending on the proportion of the species within another species buffer (Figure 2-4a - Figure 2-4c), and the strength of the Exp(β) coefficients for the variables in the species comparison models (Table 2-7). Here, I discuss seasons with high and low spatial separation in more detail.

5.2.1. Caribou and wolves

Mountain caribou and wolves experienced the highest level of spatial separation in the late winter, followed by moderate levels in the early winter and

summer. The spring and calving seasons had the lowest level of spatial separation between caribou and wolves.

Past studies also report high levels of spatial separation between caribou and wolves in the winter, when preferences in elevation (Seip 1992; Allison 1998), habitat (Seip 1992; Cumming et al. 1996; James et al. 2004), and distances from wolf travel routes were examined (Bergerud and Page 1987). Johnson et al. (2002) also found that wolves did not hunt in habitats strongly selected by caribou as foraging areas in the winter. Caribou may represent a less profitable prey choice for wolves with higher search times and lower energy return compared to moose (Bergerud et al. 1984; Adams et al. 1995a; Hayes et al. 2000; Lessard et al. 2005). A high level of spatial separation may also be attributed to the effect of snow and food availability on the distribution of caribou and wolves. In the late winter, mountain caribou ascend to higher elevations as snows deepens and consolidates, to gain access to arboreal lichen in old Englemann spruce and subalpine fir stands (Apps et al. 2001). Wolves have been shown to select valley bottoms with shallower snow depths and high concentrations of prey (Fuller 1991; Kunkel and Pletscher 2000; Callaghan 2001; Whittington et al. 2005; Hebblewhite 2006). Valley bottoms are especially important to wolves in the winter when shallower snow depths increase the efficiency of movement (Huggard 1993; Whittington et al. 2005). Strong selection of alpine by mountain caribou in this season, relative to wolves, may represent the predator avoidance strategy of 'spacing away' from wolves (e.g. Bergerud and Page 1987; Johnson et al. 2002; Mech and Peterson 2003).

My results suggested that mountain caribou and wolves had low spatial separation in the spring, similar to patterns of spatial overlap found by Neufeld (2006). In spring, mountain caribou descend to lower elevations where they use old forests and young plantations where emergent vegetation is first available (Apps et al. 2001). Overlap between caribou and wolf resource selection was evident in their similar use of high biomass areas represented by young forests (0 – 40 yrs), non-forested areas (shrub, burns) and forests-other (deciduous, Douglas fir, lodgepole pine). Wolf resource selection studies in Alberta found that wolf use is associated with cutblocks and younger forests (Neufeld 2006), and shrubby areas (Kuzyk 2002) and younger forests (Neufeld 2006). Landscapes with these attributes may represent areas of high predation risk for caribou in the spring. In particular, Wittmer (2007) found that the amount of early-seral forest best explains the variation in caribou survival rates within 10 caribou distributions across B.C. Even during seasons that represented low spatial overlap, mountain caribou selected alpine and avoided areas closer to roads than wolves. The strength of avoidance of areas within 100 m of roads was higher than the winter, therefore there may be additional avoidance not strictly attributed to elevation. The distribution of roads in the study area was constrained to areas along valley bottoms, therefore elevation and distance to low-use roads were difficult to separate in the analysis. Other studies have demonstrated caribou avoidance of roads and linear features (Cameron et al. 1992; Nellemann and Cameron 1996; Nellemann and Cameron 1998; Nellemann et al. 2001; Dyer et al. 2001; Oberg 2001). Caribou may avoid roads to reduce predation because wolves use these

features as travel routes to increase travel efficiency, especially when snow depths off the trail may hamper movement (Musiani et al. 1998; Ciucci et al. 2003; Whittington et al. 2005).

Mountain caribou and wolves experienced the lowest level of spatial separation during the calving season. During this season, mountain caribou ascend to high elevations to calve and access their summer range (Apps et al. 2001). These calving areas are often located above treeline, favouring southern slopes, heterogeneous snow cover, and rugged, mountainous terrain (Bergerud et al. 1984; Bergerud and Page 1987). My results were counter to what one would expect if caribou were spacing away from high wolf-risk areas during calving. Gustine et al. (2006) found that predation risk from gray wolves influenced where woodland caribou calve resulting in caribou avoiding areas with high biomass likely associated with increased predation risk. My results suggested that landcover and forest age attributes, representing levels of high biomass (e.g. forest age 0 – 40 yrs; non-forested areas, forest-other), were used in similar proportions by caribou and wolves. However, caribou and wolves differed in their relative selection in of alpine, old forests and rugged terrain.

There are four possible explanations why my data indicated low spatial separation between wolves and caribou during the calving season. First, wolf predation-risk may not have a strong influence on the structure of caribou habitat selection, and the influence of other predators should be considered. For instance, mountain caribou selected alpine habitats ten times as much as wolves, which is less than in other seasons, possibly due to the presence of grizzly bears in this

habitat (McLellan pers. comm.; Simpson et al. 1987). Second, wolves were successful in accessing caribou calving areas. Data on survival of caribou neonates during this season is required to determine if low spatial separation results in higher predation rates. Third, finer-scale differences in use of terrain, alpine and old forests were sufficient to maintain sufficient spatial separation between mountain caribou and wolves, even at what I considered to be low levels. Finally, my mortality data showed an increase in wolf mortalities since 2000, therefore caribou may not have had time to adjust their habitat use to account for increases in wolf-predation risk.

5.2.2. Caribou and moose

Caribou and moose had the greatest spatial separation during spring and calving seasons. Early winter and summer are seasons when spatial separation was low, followed by moderate levels in the late winter.

My results supported previous studies that demonstrate caribou and moose spatially separate themselves by using different habitats (Boonstra and Sinclair 1984; Bergerud and Page 1987; Seip 1992; Cumming et al. 1996; Boer 1998; James et al. 2004). I found that caribou and moose differed in their use of old forests (141 – 680 yrs), alpine areas, aspect and distances > 2000m from low-use roads in the spring and calving seasons. These differences in resource selection may be due to foraging differences between the two species (Boer 1998; Hofmann 2000; Dussault et al. 2005) and/or the antipredator strategy of caribou to 'space away' from predators and alternate prey species (Seip 1992; Apps et al. 2001). Roads are commonly constrained along valley bottoms in mountainous terrain, so

the low-use road variable probably functioned as a surrogate for elevation during these seasons. During calving season, the relative selection of alpine, northerly slopes and high elevations are indicative of calving site selection by mountain caribou (Bergerud et al. 1984; Bergerud and Page 1987) compared to open, upland (stream valley shrub, alluvial) and aquatic habitats selected by moose (Tefler 1984; Peek 1998).

Mountain caribou and moose experienced the lowest degree of spatial separation in the early winter and summer relative to the other seasons, although the exp(β) values were still relatively high. In the early winter, overlap in resource selection between caribou and moose occurred in forests-other, spruce/subalpine fir forests and areas within 100 m of roads. Roads may be a surrogate for elevation in this season, because mountain caribou are at low elevations in the early winter (1200 m; Apps et al. 2001), but this also places them within proximity to respond to roads. Caribou may avoid roads to reduce predation because both moose and wolves use these features as travel routes (Musiani et al. 1998; Ciucci et al. 2003; Whittington et al. 2005) and road sides may provide high-quality forage that attract moose (Peek 1998). My results were inconclusive regarding the influence of roads on the spatial distribution of caribou and moose, because I could not separate possible avoidance of roads and elevation.

Spatial separation between mountain caribou and moose was low in the summer, possibly due to the overlapping forage preferences of the two species during this season (Boer 1998), as illustrated in their similar use of landcover and

early age forests. Although there was similar use of alpine between the two species, mountain caribou selected steeper terrain and distance further from roads relative to moose.

5.2.3. Moose and wolves

Moose and wolves had the highest degree of spatial separation in the early winter and low levels of spatial separation in all other seasons. Relative to wolves, moose strongly selected areas within close proximity to cutblocks (0 – 100 m) in the early winter, presumably reflecting their requirements for high-quality forage (Cumming et al. 1996; Peek 1998; Courtois et al. 2002; Maier et al. 2005; Potvin et al. 2005). These areas may provide a refuge for moose because wolf travel is impeded by deep, unconsolidated snow (Huggard 1993) characteristic of early winter snow pack conditions in this region.

Moose and wolves had a low degree of spatial separation in all other seasons. Moose are the primary prey of wolves in this system (Seip 1992), and therefore would select habitat types that matched the habitat selection patterns and highest densities of moose in order to maximize their foraging efficiency (e.g. Kunkel et al. 2004; Hebblewhite 2006). Overlap in habitat use and elevation has also been documented between moose and wolves in other studies (e.g. Seip 1992; Cumming et al. 1996; James et al. 2004).

In the late winter, moose and wolves used landcover categories in similar proportions, with the exception of forests-other (Douglas fir, deciduous, pine). Although the strength of differences in proximity to low-use roads were weak, moose used areas closer to roads more than wolves. Areas around roads may

represent areas with reduced predation risk for wolves, if wolves avoid these areas to reduce their risk of mortality from human hunting and poaching (Kunkel and Pletscher 2000). Roads are also often built to access timber, thus are located near high quality forage habitats and with nearby hiding cover ideal for moose (Kunkel and Pletscher 2000; Dussault et al. 2005). In snow-free seasons, there were small increases in relative use by moose of spruce/subalpine fir forests, decreased use of cutblock areas, and movements away from low-use roads compared to wolves. These differences in resource selection by moose and wolves may reflect the migration of moose to higher elevations to take advantage of forage available in high-alpine dwarf shrub communities and wet subalpine forests (Edwards and Ricey 1956; Seip 1992; Peek 1998). In contrast, wolves may be constrained to lower elevations because of activities surrounding denning, and characteristics of rendevous sites (Mao et al. 2005). These sites often occur at low elevations in close proximity to rivers (Ballard and Dau 1983; Huggard 1993). This response to wolf activity has been observed in Yellowstone National Park, when elk select higher elevations, less open habitat, and more burned forests in the summer to avoid wolf activity centered around den and rendezvous areas (Mao et al. 2005). By selecting elevations above high wolf-use areas, moose can reduce their predation risk (e.g. Kunkel and Pletscher 2000). Spatial separation between moose and wolves may be lowest in the late summer because wolf packs resume their hunting forays after wolf pups are old enough to travel.

5.3. Limitations and assumptions

As with most resource selection studies, my ability to accurately predict resource selection may be affected by sample size, autocorrelation of relocations, pooling of relocation data, choice of study area size and boundaries, and number of habitats considered (Thomas and Taylor 2006; Alldredge and Griswold 2006). Telemetry data used to represent wolf resource selection could be improved by increasing sample sizes and sampling a broader distribution of wolf packs within the study area. The model representing wolf resource selection was weighted towards selection by the Goldstream pack, and I assumed that this selection was indicative of selection across wolf packs.

Three of 15 models had poor to moderate predictive ability. This could be due to selection of variables occurring at different scales than those included, exclusion of important variables, or the complete overlap of species resource selection. For example, in the moose and wolf comparison model, if there was complete overlap in resource selection, most of the variables would be highly correlated or not significant and a highly predictive model may not be found. Finally, the proportion of locations within another species buffer did not always agree with the model results and was not a useful measure of spatial separation at fine scales.

6. Conclusions

Lessard (2005) outlines the conditions by which mountain caribou can escape depensatory predation and extirpation. These conditions exist when there

is habitat differentiation between caribou and moose, caribou are not limited by amount of older forests, there is high spatial separation between caribou and moose, moose density is higher than caribou density, and predators do not dominate the scale at which caribou and moose select habitats (Lessard 2005). Caribou population declines in British Columbia and Alberta (e.g. Seip 1992; Neufeld 2006) may be due to violations in these conditions in altered habitats (Lessard 2005). Is the current anti-predator strategy of caribou in the north Columbia Mountains sufficient to avoid high rates of wolf predation in a landscape with elevated moose populations, fragmented forest patches and the conversion of mature forests to early-seral stage forests? Conditions may be satisfied in all seasons except spring and calving, where spatial separation is at its lowest between mountain caribou and moose. The majority of all predation events occur during calving and summer months in the study area (McLellan pers. comm), and province-wide (1984 – 2002; Wittmer et al. 2005), reflecting a possible failure of spatial separation as an antipredator strategy for adult caribou during these seasons. Seip (1992) also found that wolf predation occurred in the summer and early winter, and bear predation in the spring and early summer. The increase in the number of adult caribou mortalities attributed to wolves during the time period of this study (2003 – 2006), and relatively low degree of spatial separation in the spring and calving seasons, suggests failure of spatial separation to reduce predation. More data on caribou mortality sources after 2000 is required to confirm this hypothesis. Lessard (2005) also suggests that wolves may be scale dominant over prey because wolves defend large territories and have

fast movement rates, therefore reducing the effectiveness of niche differentiation between caribou and moose. Snow-free periods would therefore pose the greatest risk of spatial overlap when movement rates of wolves are highest.

Survival of mountain caribou in the north Columbia Mountains may depend on maintaining the integrity of spatial and temporal refuges and the connectivity between these refuges. For example, mountain caribou consistently selected older forests (>140 yrs) more than wolves and moose in all seasons. Wittmer (2007) found that mountain caribou killed due to predation had lower proportions of old forest and more mid-age forests in their home range when compared to surviving caribou. Therefore, these older forest age classes may represent not only a source of arboreal lichen for caribou, but a spatial refuge that minimizes predation risk from wolves. My results also showed that areas where caribou were more likely to occur than wolves were in small, isolated patches, therefore connectivity between these areas may be important. Management or recovery scenarios for caribou should focus on maintaining habitat attributes contributing to spatial separation, particularly in seasons when the probability of overlap between caribou, moose and wolves are most likely to occur.

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Table 2-1. Description of variables used in RSF models to determine differences in habitat selection between mountain caribou, moose and wolves in five seasons in the north Columbia Mountains, British Columbia between 2003-2006.

Variable		Variable type	Range of values	Description
Terrain				
	ASP	Categorical	North South	Aspect
	TRI	Continuous	0-0.38	Terrain Ruggedness Index
	SLP	Continuous	0-90 degrees	Slope
	ELEV	Continuous	345 – 3661 meters	Elevation
Habitat				
	LAND	Categorical	Cedar/hemlock Forest-other Spruce/Subalpine Fir Alpine Non-forest	Landcover type Forest-other includes forests with deciduous, pine spp. or fir as leading species. Non-forest includes non-commercial brush, cutblocks, burns and areas not currently forested.
	CRN	Continuous	0-100%	Crown closure defined as amount of ground area covered by tree crowns
	AGE	Categorical	1 (0-40) yrs 2 (41-100) yrs 3 (101-140) yrs 4 (141-650) yrs	Forest age
Human-use				
	RD_L	Categorical	1 (0-0.10) km 2 (0.10-0.50) km 3 (0.50-2.0) km 4 (>2.0) km	Distance to low-use gravel road and trail
	LOG	Categorical	1 (0-0.10) km 2 (0.10-0.50) km 3 (0.50-2.0) km 4 (>2.0) km	Distance to cutblock

Table 2-2. The results from the likelihood ratio χ^2 tests and appropriate degrees of freedom for each seasonal model for each species comparison. All models were significant with p-values <0.01.

Species Comparison	Early Winter		Late Winter		Spring		Calving		Summer	
	χ^2	df	χ^2	df	χ^2	df	χ^2	df	χ^2	df
Caribou-Wolf	1934.2	11	721.78	11	488.86	11	697.77	12	1631.43	10
Caribou-Moose	142.33	10	590.15	10	770.34	11	131.08	11	725.5	12
Moose-Wolf	59.99	4	81.21	7	636.05	14	639.97	10	21.13	3

Table 2-3. The number of telemetry locations (GPS and VHF) per season from moose, caribou and wolves from the north Columbia Mountains, British Columbia between 2003 – 2006 (EW = early winter, LW = late winter, SP = spring, CA = calving, SU = summer).

Season	Caribou	Moose	Wolf	Total
EW	2000	1435	305	3740
LW	2330	1139	305	3774
SP	1988	1048	962	3998
CA	681	359	962	2002
SU	3134	2206	962	6302

Table 2-4. Coefficients and standard errors for the most parsimonious RSF model for differences in selection in five seasons between mountain caribou and wolves in the northern Columbia Mountains, British Columbia from 2003-2006. Coefficients in bold indicate significant variables in the models. Mountain caribou are coded as one and wolves are coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*).

Variable		Early Winter		Late Winter		Spring		Calving		Summer	
		β	SE	β	SE	β	SE	β	SE	β	SE
Forest age	0-40 yrs	**-1.760**	0.335	**-2.000**	0.713	0.339	0.292	-0.113	0.59	**-0.540**	0.317
	41-100 yrs*	-	-	-	-	-	-	-	-	-	-
	101-140 yrs	**1.110**	0.242	**1.710**	0.275	**1.230**	0.332	**1.050**	0.475	**1.590**	0.446
	141-680 yrs	**3.190**	0.537	**4.420**	0.633	**1.760**	0.389	**2.080**	0.511	**2.060**	0.382
Landcover	Cedar/hemlock*	-	-	-	-	-	-	-	-	-	-
	Forest-other	**-1.490**	0.555	0.429	0.623	0.460	0.456	0.606	0.581	0.385	0.609
	SX/subalpine fir	**1.840**	0.736	**1.720**	0.676	**1.440**	0.439	**1.730**	0.396	**1.420**	0.627
	Alpine	**4.450**	1.26	**5.460**	1.53	**2.690**	0.372	**2.380**	0.425	**3.060**	0.428
	Non-forest	0.016	0.352	-0.151	0.804	0.320	0.309	0.114	0.438	**-1.010**	0.322
Road_low	0.00-0.10 km	**-1.700**	0.712	**-2.300**	0.937	**-3.260**	0.324	**-3.020**	0.324	**-4.190**	0.409
	0.10-0.50 km	-0.716	0.433	-1.160	0.650	**-2.080**	0.217	**-1.990**	0.293	**-4.370**	0.324
	0.50-2.00 km*	-	-	-	-	-	-	-	-	-	-
	> 2.00 km	**1.700**	0.817	**1.760**	0.654	**2.000**	0.554	**2.060**	0.547	**2.890**	0.632
Aspect	North*	-	-	-	-	-	-	-	-	-	-
	South	**-1.110**	0.51	-	-	-	-	-	-	-	-
Crown closure		-	-	**-0.045**	0.0125	-	-	**-0.020**	0.001	-	-
TRI		-	-	-	-	**1.770**	0.546	**2.350**	0.499	-	-
k-fold rho (P)		0.782	(<0.01)	0.748	(<0.02)	0.745	(<0.02)	0.636	(<0.05)	0.795	(<0.01)

Table 2-5. Coefficients and standard errors for the most parsimonious RSF model for differences in selection in five seasons between mountain caribou and moose in the northern Columbia Mountains, British Columbia from 2003-2006. Coefficients in bold indicate significant variables in the models. Mountain caribou are coded as one and moose are coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*).

Variable		Early Winter		Late Winter		Spring		Calving		Summer	
		β	SE	β	SE	β	SE	β	SE	β	SE
Forest age	0-40 yrs	**-1.920**	0.295	-0.022	0.937	0.324	0.650	-0.091	0.708	-0.465	0.290
	41-100 yrs*	-	-	-	-	-	-	-	-	-	-
	101-140 yrs	**0.601**	0.230	0.685	0.401	**1.220**	0.419	0.167	0.596	**0.850**	0.313
	141-680 yrs	**2.270**	0.300	**2.850**	0.693	**2.850**	0.418	**1.860**	0.520	**1.780**	0.548
Landcover	Cedar/hemlock*	-	-	-	-	-	-	-	-	-	-
	Forest-other	**-2.020**	0.819	1.100	1.050	-0.594	0.546	1.010	0.606	1.150	0.657
	SX/subalpine fir	1.240	0.663	**2.420**	0.930	0.443	0.679	0.535	0.550	0.288	0.665
	Alpine	**3.280**	0.950	**5.050**	1.370	**3.530**	1.020	**3.390**	0.851	1.220	0.995
	Non-forest	**-1.040**	0.297	-0.032	1.100	0.248	0.740	-0.313	0.551	-0.852	0.816
Road_low	0.00-0.10 km	-1.220	0.864	**-0.740**	0.249	-0.145	0.276	0.313	0.579	0.661	0.505
	0.10-0.50 km	**2.860**	0.467	**2.960**	0.643	**2.970**	0.363	1.230	0.642	**2.820**	0.330
	0.50-2.00 km*	-	-	-	-	-	-	-	-	-	-
	> 2.00 km	**5.030**	1.540	**6.400**	1.010	**7.320**	1.220	**7.180**	1.400	**5.540**	0.653
Aspect	North*	-	-	-	-	-	-	-	-	-	-
	South	-	-	-	-	**-1.120**	0.446	**-1.590**	0.432	**-0.950**	0.465
TRI		-	-	-	-	-	-	-	-	**2.120**	2.120
k-fold rho (*P*)		0.669	(<0.05)	0.685	(<0.05)	0.644	(<0.05)	0.653	(<0.05)	0.833	(<0.01)

Table 2-6. Coefficients and standard errors for the most parsimonious RSF model for differences in selection in five seasons between moose and wolves in the northern Columbia Mountains, British Columbia from 2003-2006. Coefficients in bold indicate significant variables in the models. Moose are coded as one and wolves are coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*).

Variable		Early Winter		Late Winter		Spring		Calving		Summer	
		β	SE	β	SE	β	SE	β	SE	β	SE
Forest age	0-40 yrs	-	-	-	-	0.430	0.383	-	-	-	-
	41-100 yrs*	-	-	-	-	-	-	-	-	-	-
	101-140 yrs	-	-	-	-	-0.248	0.336	-	-	-	-
	141-680 yrs	-	-	-	-	**-1.420**	0.501	-	-	-	-
Landcover	Cedar/hemlock*	-	-	-	-	-	-	-	-	-	-
	Forest-other	-	-	**-1.060**	0.482	0.851	0.768	-0.062	0.734	-	-
	SX/subalpine fir	-	-	-0.563	0.681	**0.527**	0.256	**1.170**	0.527	-	-
	Alpine	-	-	-0.363	2.05	**-2.340**	1.03	-1.100	0.922	-	-
	Non-forest	-	-	-0.816	0.621	-0.208	0.424	**1.100**	0.308	-	-
Cutblock	0.00-0.10 km	**5.210**	0.771	-	-	**-1.720**	0.771	-1.510	0.96	-0.641	0.446
	0.10-0.50 km	**3.740**	0.756	-	-	**-1.450**	0.756	-0.910	0.793	**-1.220**	0.385
	0.50-2.00 km*	-	-	-	-	-	-	-	-	-	-
	> 2.00 km	**2.440**	1.030	-	-	**-4.480**	1.03	-1.490	0.889	0.172	0.383
Road_low	0.00-0.10 km	-	-	**1.450**	0.536	0.795	0.654	**-1.800**	0.580	-	-
	0.10-0.50 km	-	-	**1.710**	0.449	**1.400**	0.535	**-0.930**	0.353	-	-
	0.50-2.00 km*	-	-	-	-	-	-	-	-	-	-
	> 2.00 km	-	-	-1.360	1.060	-2.570	1.43	**-3.930**	1.27	-	-
Aspect	North*	-	-	-	-	-	-	-	-	-	-
	south	-	-	-	-	**1.160**	0.525	-	-	-	-
Slope		-0.041	0.0215	-	-	-	-	-	-	-	-
k-fold rho (P)		0.901	(<0.002)	0.141	ns	0.647	(<0.05)	0.572	(<0.1)	0.515	(<0.2)

ns = not significant

Table 2-7. The Exp(β) of the most parsimonious RSF models used in the interpretation of the differences in selection in five seasons between mountain caribou, moose and wolves in the northern Columbia Mountains, British Columbia from 2003-2006 (EW = early winter, LW = late winter, SP = spring, CA = calving, SU = summer). Significant variables are highlighted in bold. The first species in the comparison heading is coded as one and the second is coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*).

		Caribou and Wolf Comparison					**Caribou and Moose Comparison**					**Moose and Wolf Comparison**				
Variable		EW	LW	SP	CA	SU	EW	LW	SP	CA	SU	EW	LW	SP	CA	SU
Age	0-40	**5.81**	**7.39**	1.40	1.12	**1.72**	**6.82**	1.02	1.38	1.09	1.59	-	-	1.54	-	-
	41-100*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	101-140	**3.03**	**5.53**	**3.42**	**2.86**	**4.90**	**1.82**	1.98	**3.39**	1.18	**2.34**	-	-	1.28	-	-
	141-680	**24.29**	**83.10**	**5.81**	**8.00**	**7.85**	**9.68**	**17.29**	**17.29**	**6.42**	**5.93**	-	-	**4.14**	-	-
Landcover	CW/HW*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Forest	**4.44**	1.54	1.58	1.83	1.47	**7.54**	3.00	1.81	2.75	3.16	-	**2.89**	2.34	1.06	-
	SX/BL	**6.30**	**5.58**	**4.22**	**5.64**	**4.14**	3.46	**11.25**	1.56	1.71	1.33	-	1.76	**1.69**	**3.22**	-
	Alpine	**85.63**	**235.10**	**14.73**	**10.80**	**21.33**	**26.58**	**156.0**	**34.12**	**29.67**	3.39	-	1.44	**10.38**	3.00	-
	Non-forest	1.02	1.16	1.38	1.12	**2.75**	**2.83**	1.03	1.28	1.37	2.34	-	2.26	1.23	**3.00**	-
Cutblock	0.0-0.1	-	-	-	-	-	-	-	-	-	-	**183.1**	-	**5.58**	4.53	1.90
(km)	0.1-0.5	-	-	-	-	-	-	-	-	-	-	**42.10**	-	**4.26**	2.48	**3.39**
	0.5-2.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	> 2.0	-	-	-	-	-	-	-	-	-	-	**11.47**	-	**88.23**	4.44	1.19
Road_low	0.0-0.1	**5.47**	**9.97**	**26.05**	**20.49**	**66.02**	3.39	**2.10**	1.16	1.37	1.94	-	**4.26**	2.21	**6.05**	-
(km)	0.1-0.50	2.05	3.19	**8.00**	**7.32**	**79.04**	**17.46**	**19.30**	**19.49**	3.42	**16.78**	-	**5.53**	**4.06**	**2.53**	-
	0.5-2.0*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	> 2.0	**5.47**	**5.81**	**7.39**	**7.85**	**17.99**	**152.9**	**601.9**	**1510**	**1313**	**254.7**	-	3.90	13.07	**50.91**	-
Aspect	North*						-	-	-	-	-	-	-	-	-	-
	South	**3.03**					-	-	**3.06**	**4.90**	**2.59**	-	-	**3.19**	-	-
Crown Closure		-	**1.05**		**1.02**		-	-	-	-	-	-	-	-	-	-
TRI		-	-	**5.87**	**10.49**		-	-	-	-	**8.33**	-	-	-	-	-
Slope		-	-	-	-	-	-	-	-	-	-	1.04	-	-	-	-

Table 2-8. The degree of spatial separation (H = high, M = moderate, L = low) for three species comparisons in five seasons in the north Columbia Mountains, British Columbia.

Species Comparison	Season				
	Early Winter	Late Winter	Spring	Calving	Summer
Caribou-Wolf	M	H	L	L	M
Caribou-Moose	L	M	H	H	L
Moose-Wolf	H	L	L	L	L

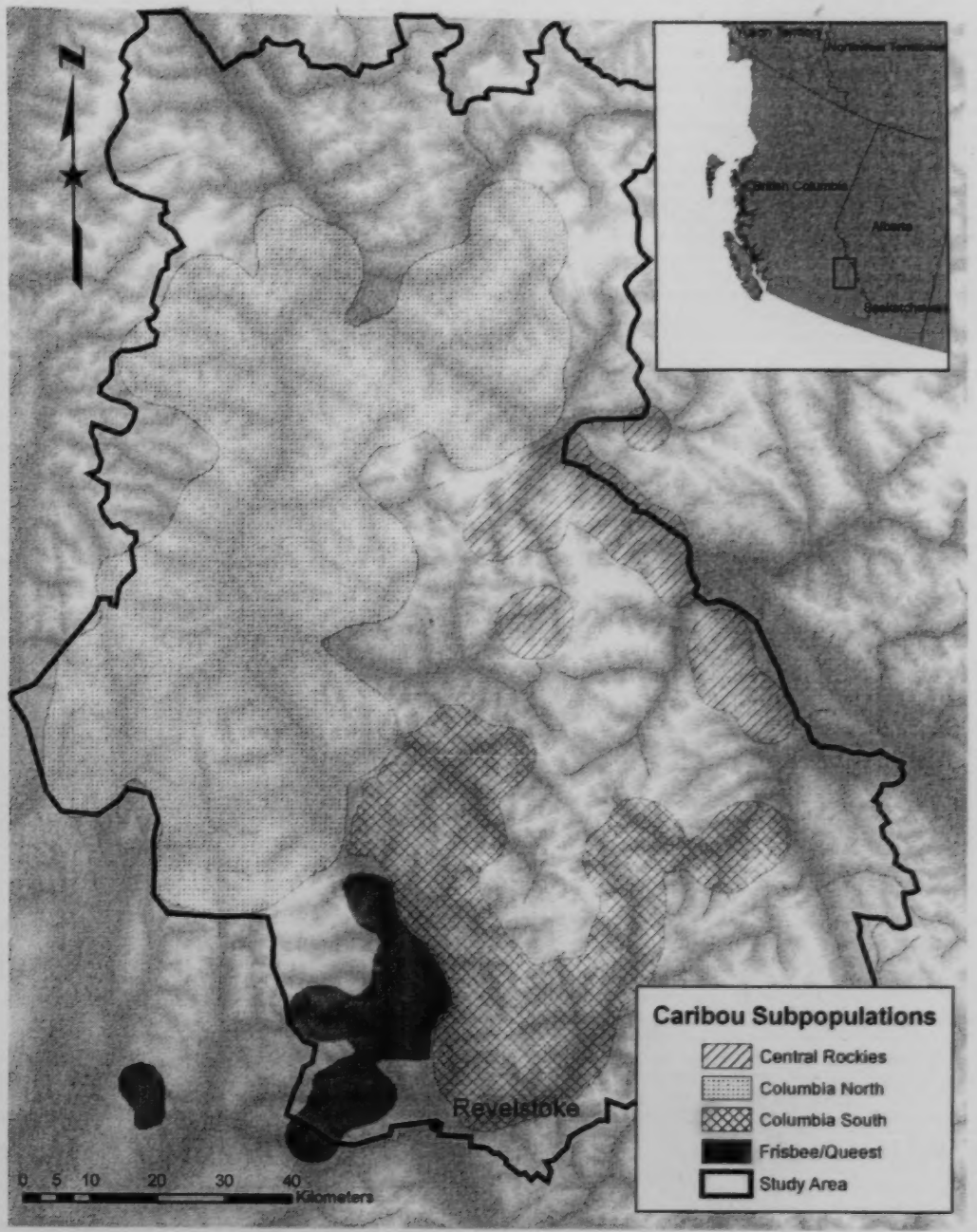


Figure 2-1. Outline of the study area encompassing the north Columbia Mountains, British Columbia, Canada. Mountain caribou subpopulations in the study area include Central Rockies, Columbia North, Columbia South and Frisbee/Queest (Wittmer et al. 2005).

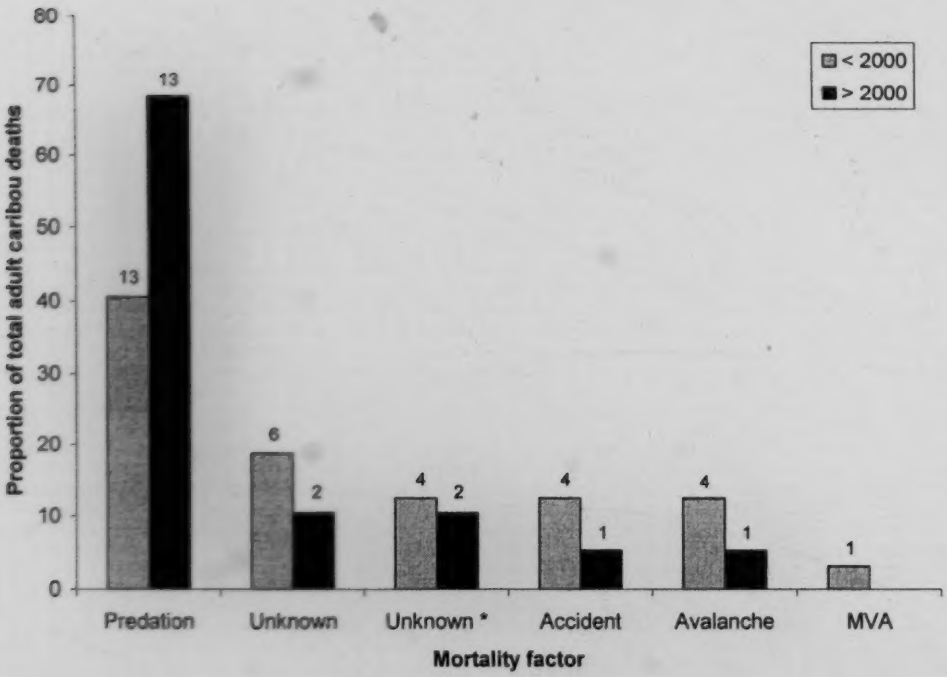


Figure 2-2. Mortality factors of adult radio-collared mountain caribou in the north Columbia Mountain study area, British Columbia from < 2000 (1992 - 1999) and > 2000 (2000 – 2006). Proportions were corrected for caribou sampling effort (number of caribou years) during each time period. The number above the bars indicated the raw number of mortalities within each mortality category. * Non-predation related unknown mortalities. MVA = motor vehicle accidents. Accident = natural disasters such as tree fall and rock crevasses.

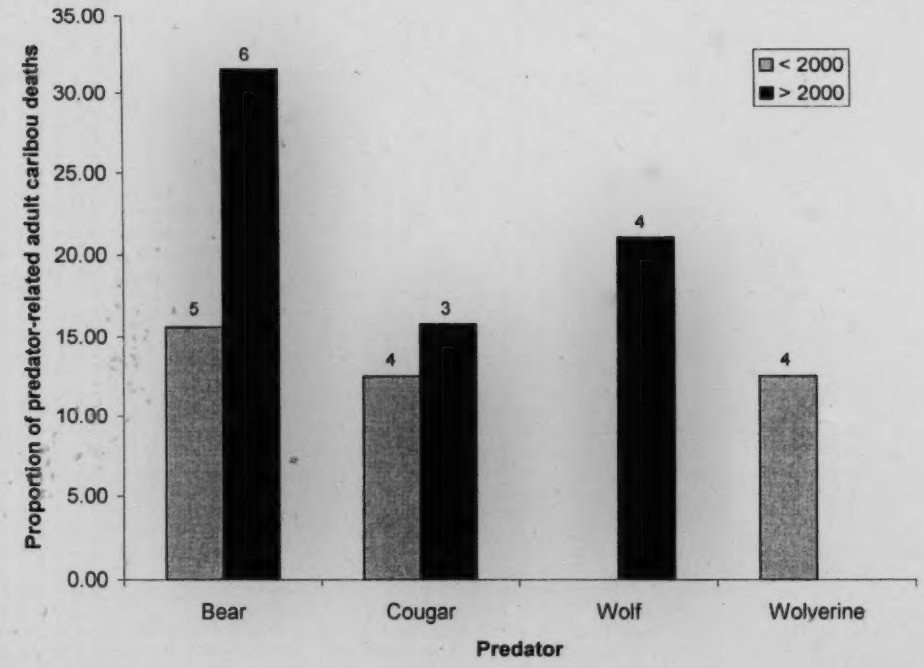
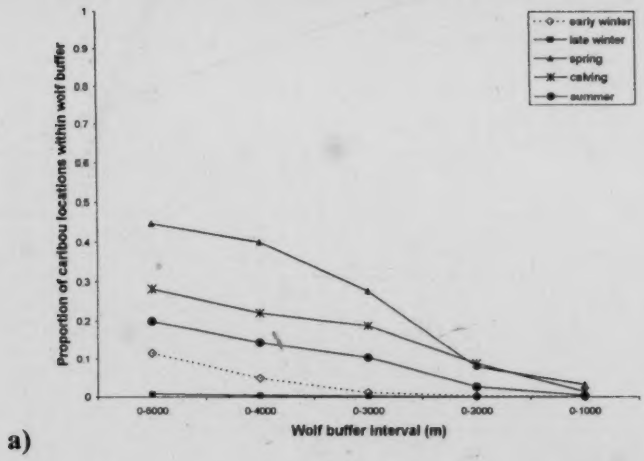
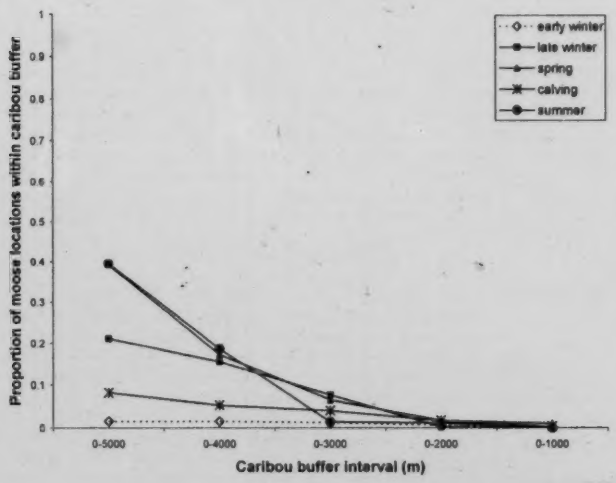


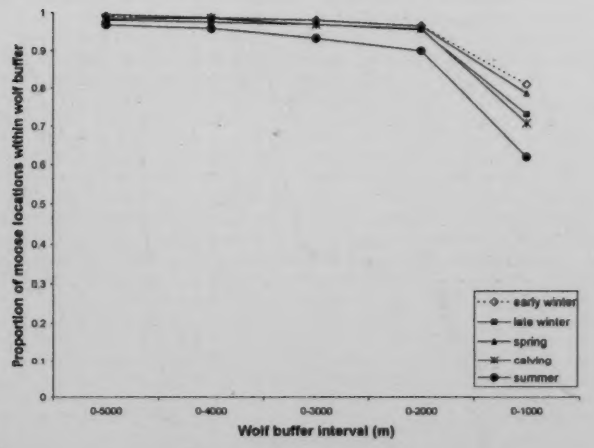
Figure 2-3. Mortality factors of predation-related adult radio-collared mountain caribou in the north Columbia Mountain study area, British Columbia from < 2000 (1992 - 1999) and > 2000 (2000 – 2006). Proportions were corrected for caribou sampling effort (number of caribou years) during each time period. The number above the bars indicated the raw number of mortalities within each mortality category.



a)

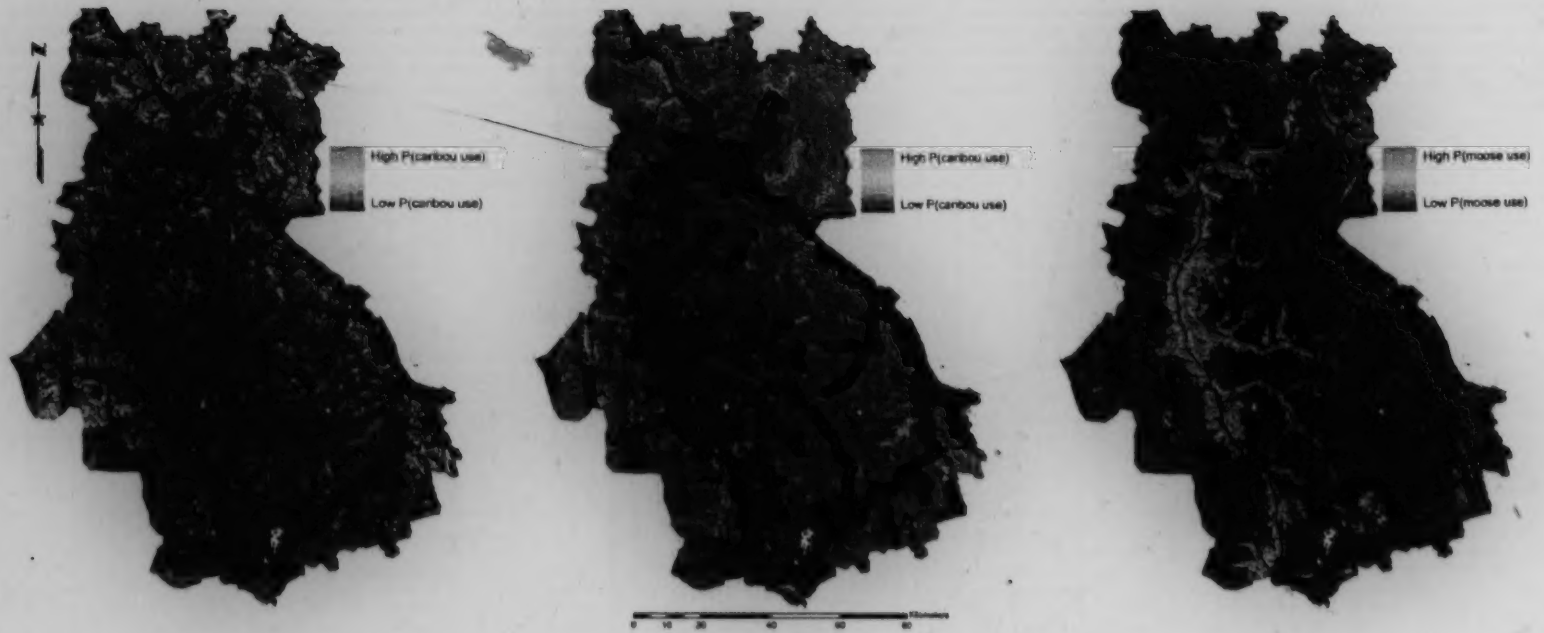


b)



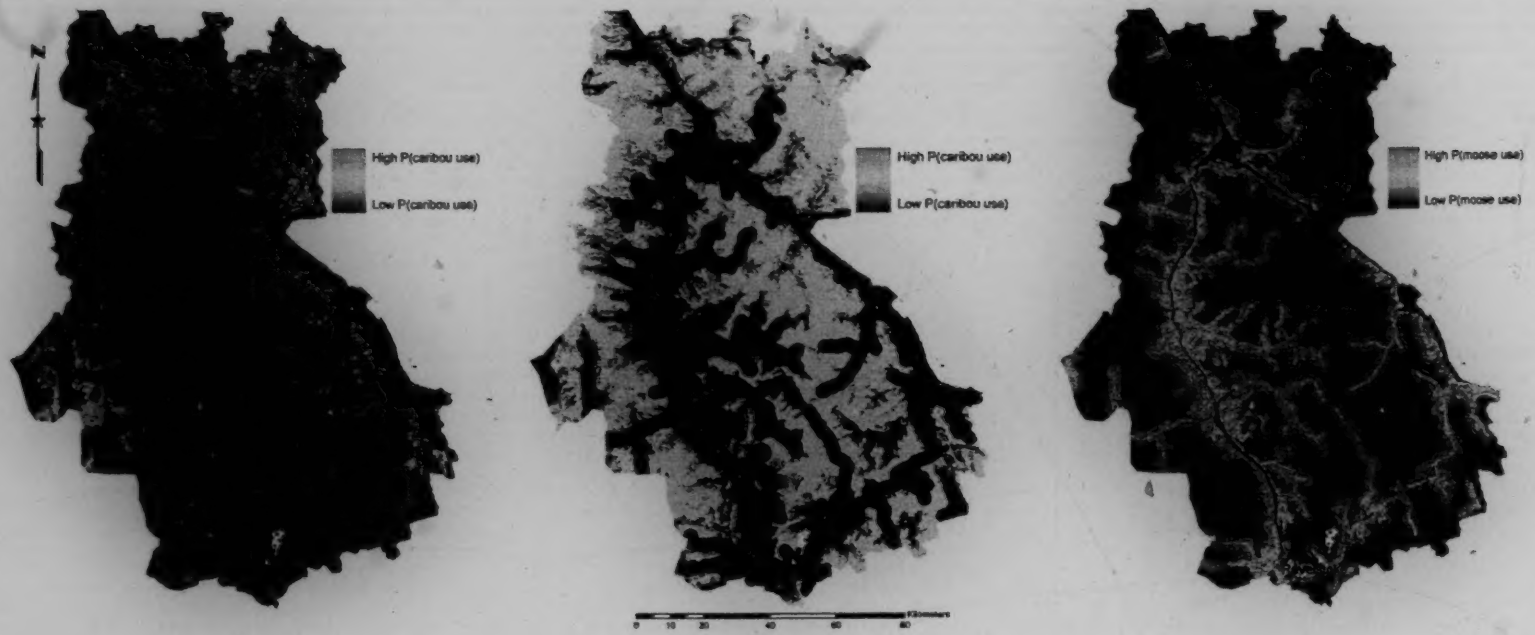
c)

Figure 2-4. The proportion of telemetry locations for mountain caribou and moose falling within 1000 m buffers of wolves, and each other, for five seasons in the north Columbia mountains, British Columbia from 2003-2006.



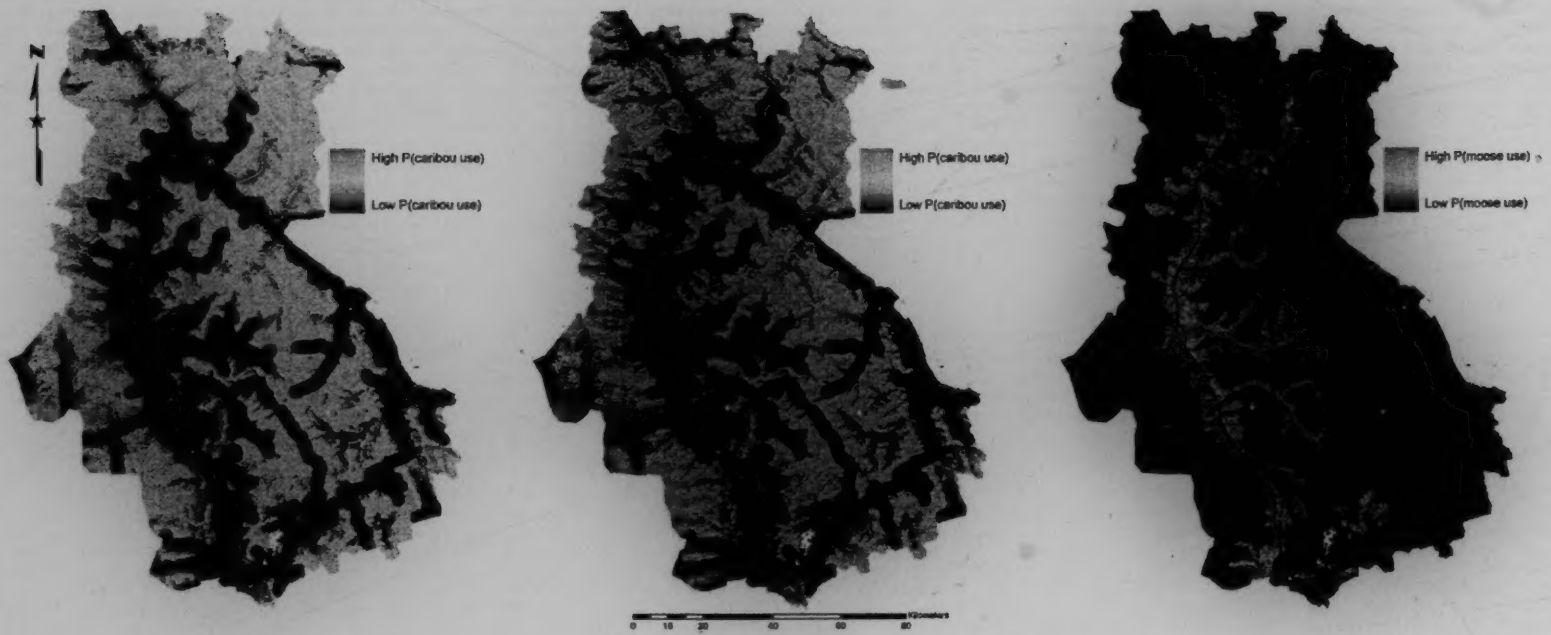
a) caribou and wolves b) caribou and moose c) moose and wolf

Figure 2-5. Differences in resource selection between mountain caribou, wolves and moose in the early winter season from 2003-2006 in the north Columbia Mountains, British Columbia.



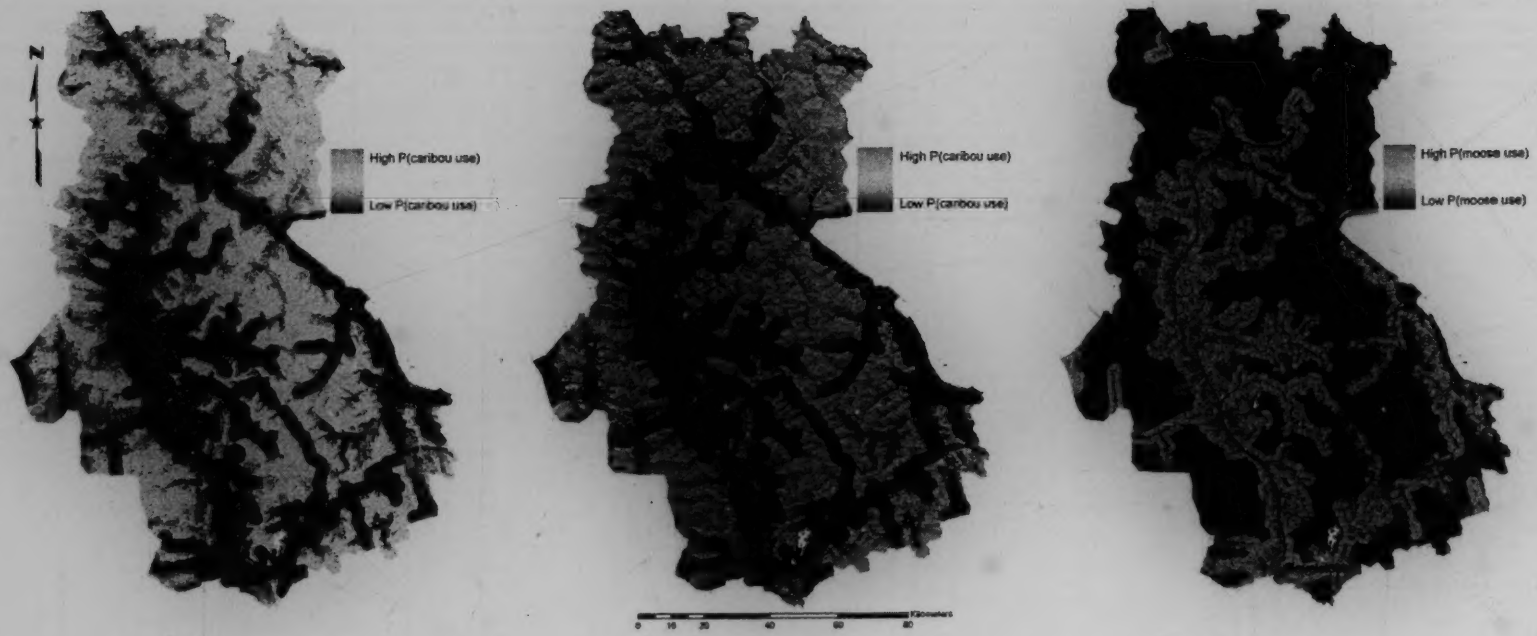
a) caribou and wolves b) caribou and moose c) moose and wolf

Figure 2-6. Differences in resource selection between mountain caribou, wolves and moose in the late winter season from 2003-2006 in the north Columbia Mountains, British Columbia.



a) caribou and wolves b) caribou and moose c) moose and wolf

Figure 2-7. Differences in resource selection between mountain caribou, wolves and moose in the spring season from 2003-2006 in the north Columbia Mountains, British Columbia.

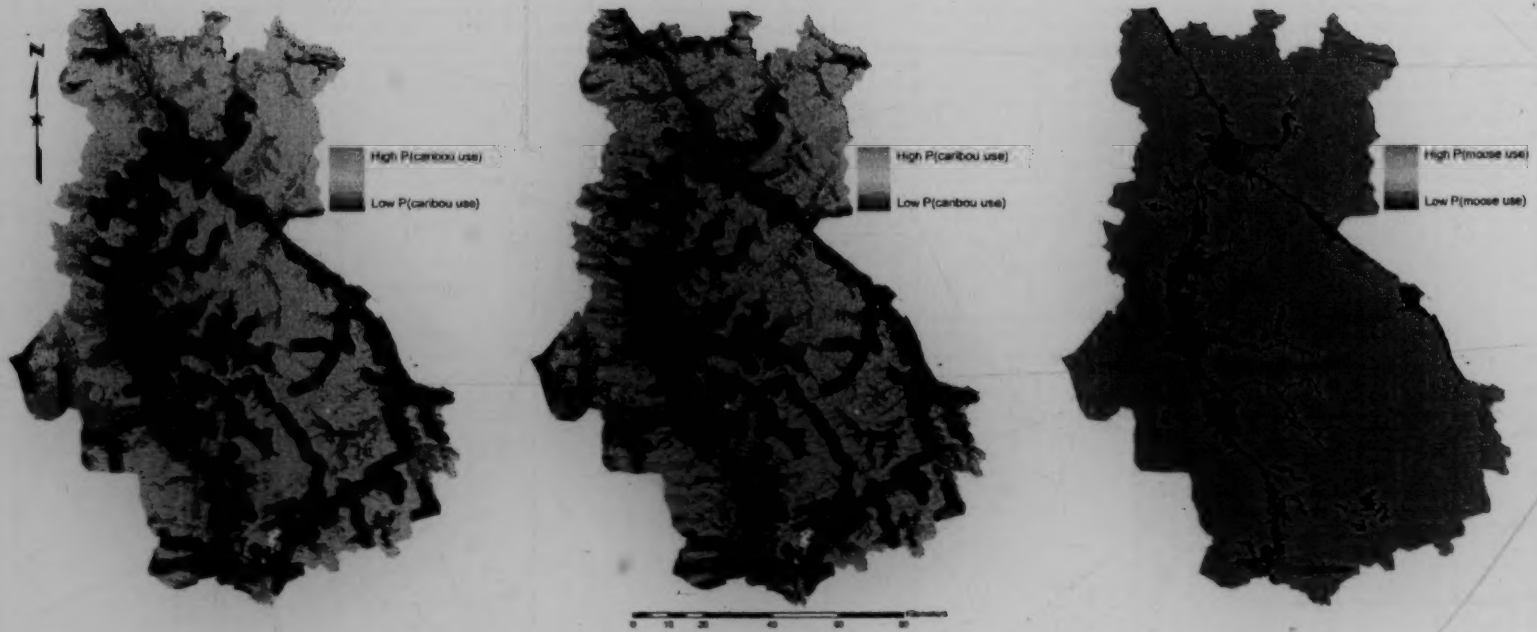


a) caribou and wolves

b) caribou and moose

c) moose and wolf

Figure 2-8. Differences in resource selection between mountain caribou, wolves and moose in the calving season from 2003-2006 in the north Columbia Mountains, British Columbia.



a) caribou and wolves b) caribou and moose c) moose and wolf

Figure 2-9. Differences in resource selection between mountain caribou, wolves and moose in the summer season from 2003-2006 in the north Columbia Mountains, British Columbia.

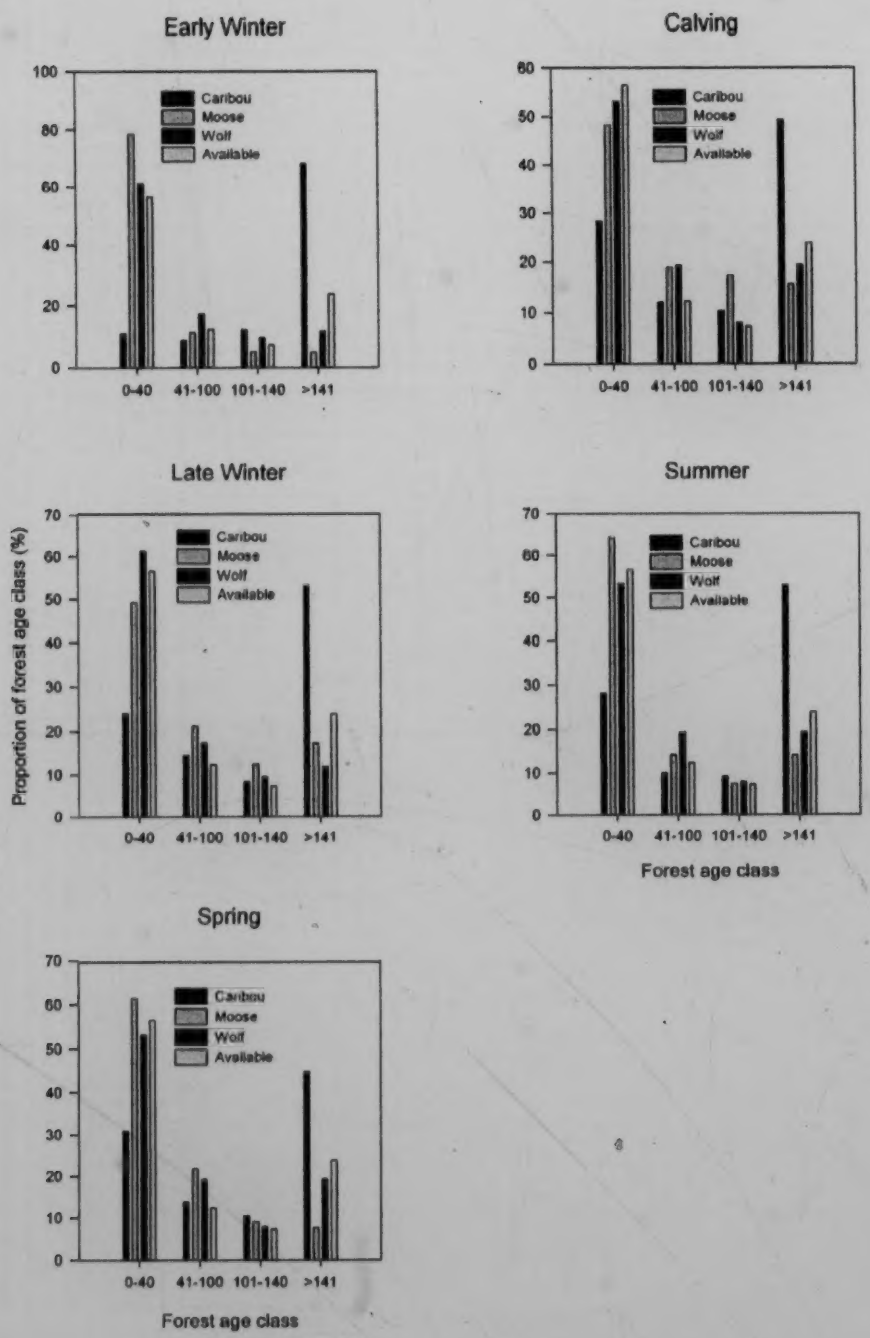


Figure 2-10. The available and marginal use of forest age classes for caribou, moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006.

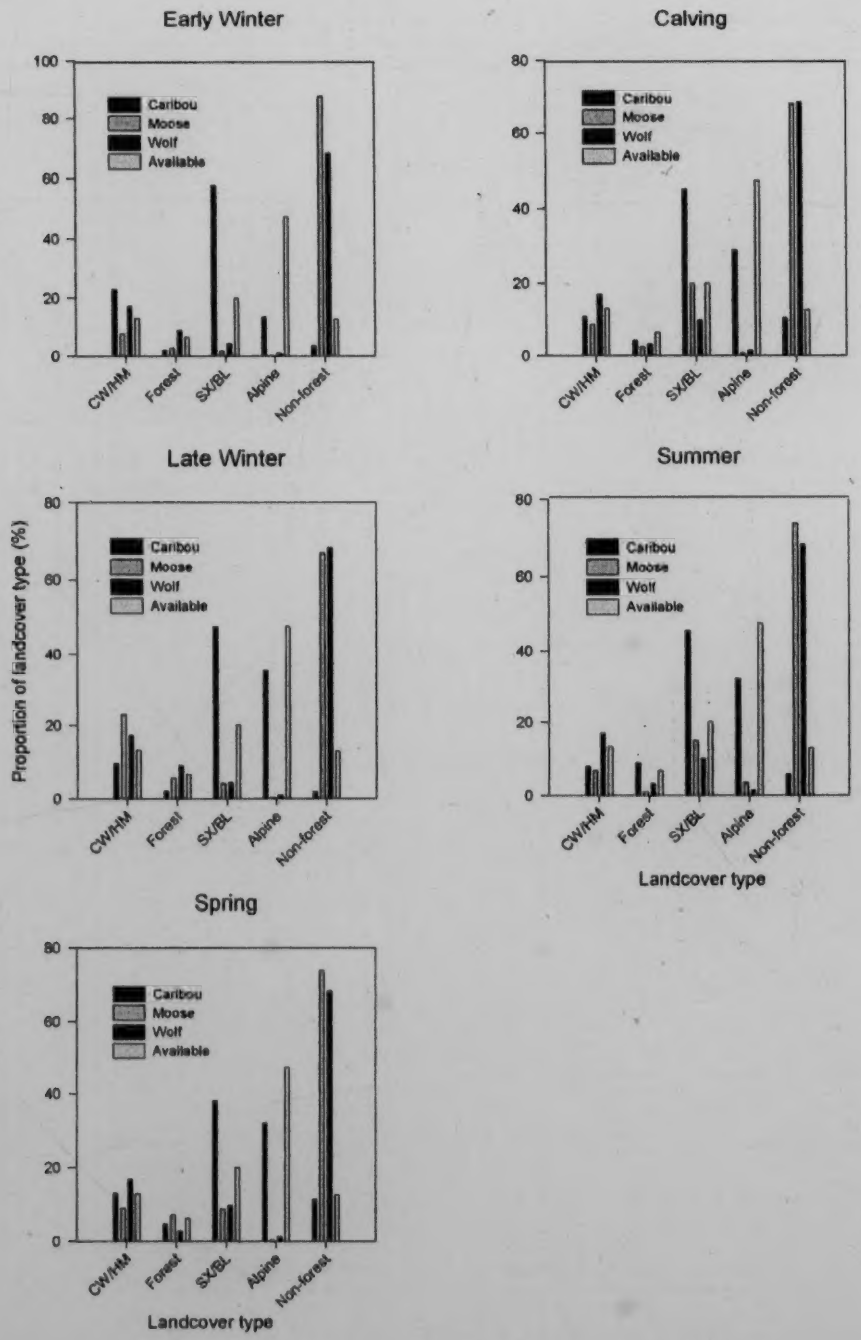


Figure 2-11. The available and marginal use of landcover for caribou, moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006.

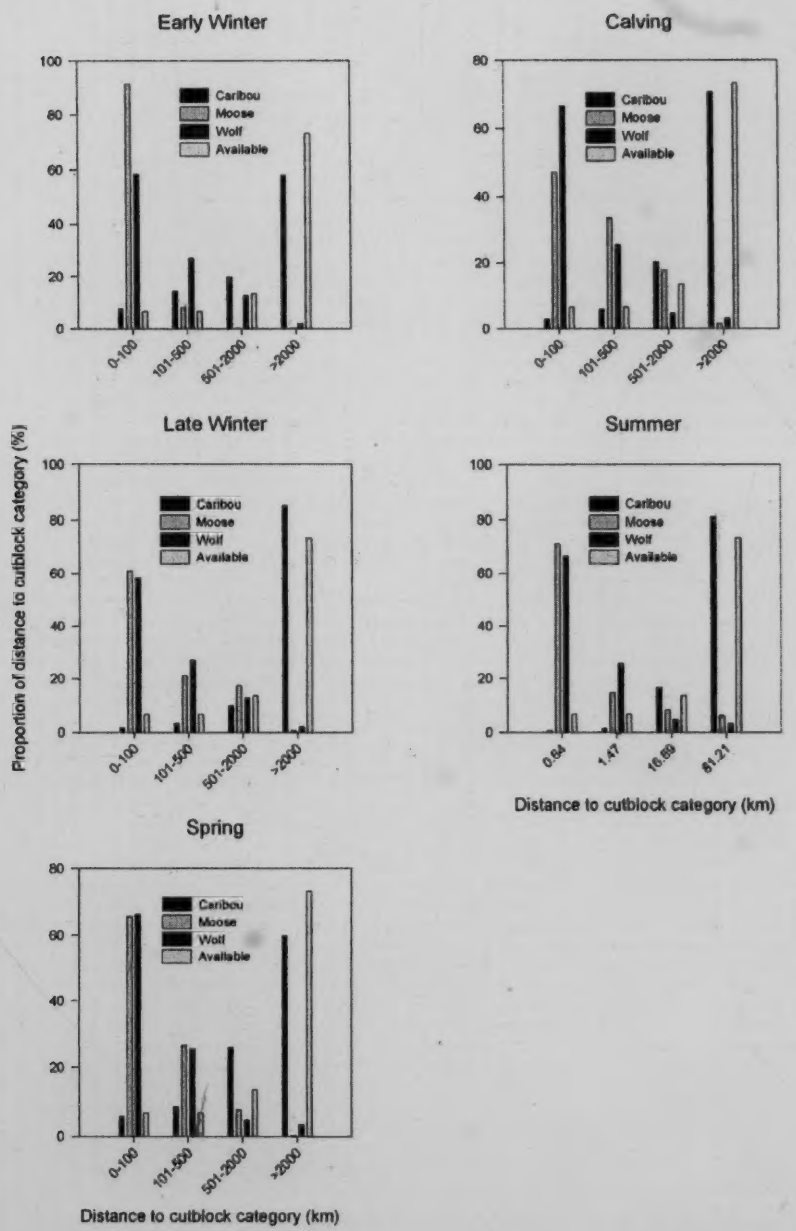


Figure 2-12. The available and marginal use of distance to cutblock category for moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006.

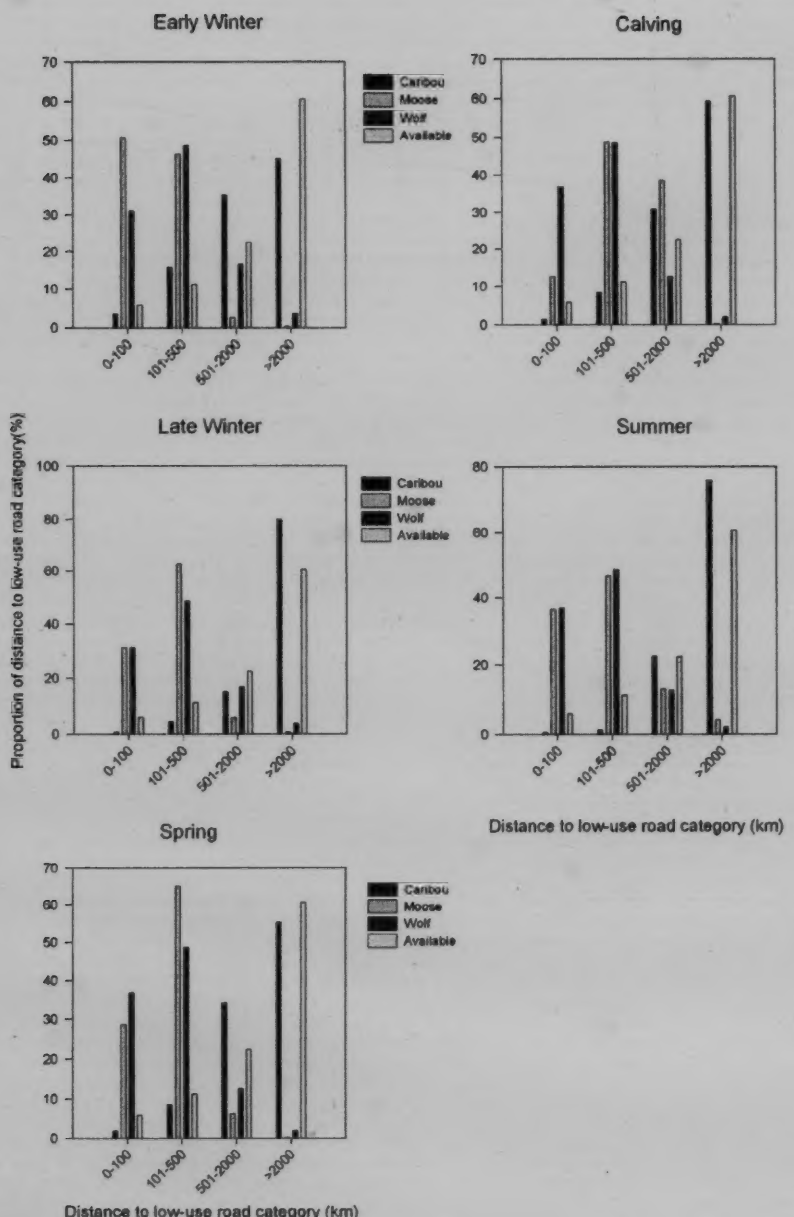


Figure 2-13. The available and marginal use of distance to low-use road category for caribou, moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006.

Chapter 3: Seasonal and pack variation in wolf diet using stable isotope analysis: implications for mountain caribou recovery

1. Introduction

Woodland caribou (*Rangifer tarandus tarandus*) are listed as "threatened" in Canada (Committee on the Status of Endangered Wildlife in Canada) due to small, declining populations and fragmented distributions. Predation is identified as the primary cause of adult mortality for a number of these populations (e.g. Stuart-Smith et al. 1997; Rettie and Messier 1998; Wittmer et al. 2005). In the north Columbia Mountains, British Columbia (B.C.), mountain caribou (arboreal lichen-feeding ecotype of woodland caribou) live in areas that overlap wolf (*Canis lupus*) and moose (*Alces alces*) distributions. During the last decade, moose densities in the area have doubled, supported by an increase in the proportion of young seral stage forests on the landscape (Poole and Serrouya 2003). Concerns that changes in species composition and abundance will exacerbate population declines and extinction of mountain caribou through "apparent competition" (Holt 1977; Holt and Lawton 1994; Wittmer et al. 2007) have focused research on predator-prey dynamics, with particular emphasis on the diet of predators.

Determining the diet of predators can be accomplished using a number of approaches, such as direct observation, analysis of stomach contents, and fecal analysis (Kelly 2000). These traditional methods for dietary reconstruction can be

logistically difficult and prone to bias depending on the method of collection and analysis (Kelly 2000). For instance, analyzing stomach contents may not be possible or appropriate for rare species and it fails to take into account different digestibility of prey items (Kelly 2000). Scat analysis may be limited by the researcher's ability to detect and collect representative samples with an appropriate sample size, and at the desired scale of investigation (Hobson et al. 2000; Mowat and Heard 2006). Scat analysis also does not account for unequal digestibility of prey items and fails to measure actual nutrients incorporated in the tissues (Hobson et al. 2000; Mowat and Heard 2006).

Stable isotope analysis is a long-standing, scientific method in the fields of geology, physiology, and atmospheric science, and more recently has been applied in ecological studies (Peterson and Fry 1987; Hobson and Wassenaar 1999). With respect to dietary reconstruction, Deniro and Epstein (1978, 1981) demonstrated that different ^{13}C and ^{15}N isotope signatures could be used to determine the relative contribution of foods to an animal's diet. Specifically, dietary analysis is based on the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ incorporated into tissue relative to a standard (Deniro and Epstein 1978, 1981; Peterson and Fry 1987). This isotope enrichment rate differs between types of tissues (Deniro and Epstein 1978) and trophic levels (Minagawa and Wada 1984). These characteristics allow scientists to address questions regarding diet spanning different time scales (e.g. Ben-David et al. 1997; Darimon and Reimchen 2002), and trophic relationships (e.g. Hobson et al. 1994; Hobson et al. 1997; Hobson et al. 2000; Kelly 2000; Urton and Hobson 2005).

Stable isotope analysis has many advantages over traditional field methods of dietary analysis (Hobson et al. 1994; Hobson et al. 2000; Litvaitis 2000). Analysis of hair and tissue measures assimilated nutrients, can designate species specific information to samples, and provides long-term to short-term windows into an animal's diet (Deniro and Epstein 1978; Mowat and Heard 2006). Collection can be inexpensive, since samples may be easily obtained using non-intrusive methods, and studies can extend over large areas and long time frames.

Using stable isotopes for dietary reconstructions has the added advantage of providing time-integrated dietary information, depending on what tissues are used for the analysis (Hobson et al. 1996; Kelly 2000). Different tissues have different metabolic rates that determine the turnover rates of stable isotopes (Hobson and Clark 1992). For instance, blood plasma reflects the isotopic signature of the foods consumed during the past 10 – 14 days (Hilderbrand et al. 1996), while bone collagen reflects the assimilation of food items over a lifetime (Szepanski et al.1999). Turnover rates of whole blood ranges from a half-life of 3.9 – 31.5 days for birds (Hobson and Clark 1992; Haramis et al. 2001; Bearhop et al. 2002; Pearson et al. 2003; Ogden et al. 2004), 34.7 days for black bears (*Urus americanus*; Hilderbrand et al. 1996), and 120 – 126 days for bats (Voigt et al. 2003). Metabolically inactive tissues such as hair, skin, whiskers, nails, and feathers reflect the diet during the time of growth (Hobson et al. 1996; Urton and Hobson 2005). For example, wolf hair collected in the winter reflects the diet from late spring to late fall (4-5 mo.; Darimont and Reimchen 2002). Multiple samples from different sampling intervals are useful for studying switching

between alternative food sources or shifts in diet to take advantage of seasonally occurring resources (Ben-David et al. 1997; Roth and Hobson 2000; Darimont and Reimchen 2002).

Stable isotope methods estimate relative dietary proportions, not absolute amounts of foods consumed. Nevertheless, theoretical predation models can provide a framework for developing hypotheses about expected proportions of prey in the diet of predators. These models, based on controlled experiments, suggest that the diet of predators is not always proportional to the relative abundance of prey in the environment (Gendron 1987; Allen 1988). For example, predators can take an excess of prey when that prey type is common (positive frequency-dependence) or a disproportionate amount of a prey type when it is less common (negative frequency-dependence; Gendron 1987; Allen 1988; Marini and Weale 1997). The primary mechanisms behind frequency-dependent predation are behavioural, having to do with components of predation risk (Gendron 1987). These include behaviours that influence encounter rates, and the probability of detecting, encountering, attacking and capturing prey (Gendron 1987; Whelan et al. 2003). Ultimately, frequency-dependent predation is influenced by the density of the different prey types and the diversity of prey in the environment (Marini and Weale 1997). When predation occurs in a system with more than one prey type, direct interactions between predator and prey can have indirect consequences for a secondary prey species, sometimes resulting in its decline or extinction (Holt 1977; Holt and Lawton 1994; Courchamp et al. 2000).

I measured stable carbon and nitrogen isotope ratios in the hair and whole blood of grey wolves in the North Columbia Mountains, British Columbia to determine the relative importance of caribou and moose in the diet of wolves. This research is important not only as a baseline to measure future change, but useful at present to elucidate the potential impact that wolves have on mountain caribou and moose populations. My objectives were to: 1) describe average wolf pack diet, 2) describe variation in diet by wolf pack and season (late spring, late fall, late winter), 3) explore the relationship between percent caribou within wolf diet and density of caribou available to each wolf pack, and 4) estimate expected amount of caribou in wolf diet from available literature, to give context to stable isotope results. I predicted that wolves would display predation characteristics indicative of a positive frequency-dependent predation model where they would concentrate on common prey types (moose) and overlook rare ones (caribou, deer). The relative proportion of caribou in the diet of wolf packs should vary by season because caribou vary in their spatial separation with wolves (Chpt 2; Seip 1992). The proportion of moose in the diet of wolf packs should not vary by season due to relatively low spatial separation in all seasons (Chpt 2). The proportion of caribou in wolf pack diets should be independent of caribou density, because caribou are rare and encounters with wolves would occur at random. While, I can not directly address whether frequency-dependent predation occurred, the use of stable isotopes to measure diet composition of predators along with corresponding densities of prey will contribute to the body of knowledge on this topic.

2. Study Area

The study area (~9,000 km^2) was located in the Northern Columbia Mountain ecoregion in southeastern British Columbia (51°N 118°W; Figure 3-1; Demarchi 1996). Rugged, mountainous terrain (550 m to 3,050 m) and high precipitation levels (946 mm/yr, 425 cm falling as snow) characterized the area. The landscape was a mosaic of forests, regenerating clear-cuts, riparian forests, shrublands, upper elevation basins, and avalanche chutes. Biogeoclimatic subzones range from Interior Cedar-Hemlock (ICH) in the valley bottoms and mid-elevations, to Engelmann Spruce-Subalpine Fir (ESSF) at approximately 1,280 m to 1,400 m (Braumandl and Curran 1992). The Alpine Tundra subzone occurs at elevations above the ESSF.

Western red cedar (*Thuja plicata)*, and western hemlock (*Tsuga heterophylla*) dominate the ICH subzones, whereas Douglas-fir (*Pseudotsuga menziesii*) is less common. The ESSF zone consists of coniferous forests comprised primarily of Englemann Spruce (*Picea Engelmannii*) and subalpine fir (*Abies lasiocarpa*). Alpine meadows, shrublands, snowfields, glaciers and rock dominate the Alpine Tundra zone. Two hydroelectric developments, in 1973 and 1984, flooded most of the low elevation riparian habitat and significantly altered the study area (BC Hydro 2007). Forest harvesting, silviculture, hunting, trapping, snowmobiling and heliskiing were the major human-use activities during the time frame of this study. Currently, 60% of merchantable forests is less than 30 years old and 40% is over 200 years old (R. Serrouya, pers. comm.)

Moose was the most abundant and widespread ungulate species (0.17 – 3.54 moose/km^2; Poole and Serrouya 2003), however low densities of mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*) and elk (*Cervus canadensis*) occurred in the southern portion of the study area. Mountain goats (*Oreamnos americanus)* also inhabited the more mountainous regions. Mountain caribou existed at low densities (0.035 - 0.05 caribou/km^2; Wittmer et al. 2005), and were delineated into four subpopulations (Columbia North, Columbia South, Frisby/Queest and Central Rockies; Wittmer et al. 2005). Grizzly bears (*Ursus arctos*), black bears, wolverine (*Gulo gulo*), wolves, and cougars (*Puma concolor*) occurred throughout the study area. Information on predator densities was not available at the time of this study.

3. Methods

3.1. Sample collection

Between 2003 to 2006, I collected guard hair from four mammalian species [deer, moose, caribou, and beaver (*Castor canadensis*)] during helicopter captures and kill site investigations, and from road mortalities and hunter kills. These species represented the main prey of wolves, as indicated by previous faecal analysis and winter tracking (Allison 1998; Stotyn et al. 2005). The stable isotope value for deer was an average of isotope values from the literature (Hobson et al. 2000) and samples from the study area. Other prey items, such as hoary marmot, red-backed vole, red squirrel, grouse, snowshoe hare, and deer mouse, made up 11.6% and 6.4% of the biomass of wolf diet items in the summer

and winter, respectively, based on faecal analysis (Allison 1998). Plant materials and berries may also contribute to wolf diet, but the effect of these sources on the isotopic signature of wolves would be negligible, because plants are poor sources of nitrogen and most of the carbon is evolved as CO_2 (Urton and Hobson 2005). I collected hair and blood samples from 28 adult wolves in five packs during helicopter netgun captures (Bighorn Helicopters Inc., Cranbrook, B.C), and from ground trapping, mortality investigations, hunter kills and road mortalities.

I rinsed hair samples three times with a 2:1 methanol:chloroform solution and dried them for 24 hrs under a fume hood (Darimont and Reimchen 2002, Urton and Hobson 2005). To capture possible seasonal variation in wolf diet, I severed wolf guard hairs into equal base and tip segments to represent late spring (tip) and late fall (base; Darimont and Reimchen 2002). I followed this procedure for five of the 28 wolf hair samples. I also collected blood samples from wolves during March 2004 – 2006 to represent late winter diet. These blood samples corresponded to a 70-day window before the date of collection (e.g. late winter; Hilderbrand et al. 1996). I estimated this time window by selecting a species with similar metabolic rates to wolves with published whole blood turnover rates. Therefore, I used black bear turnover rates and doubled the whole blood half-life estimate of 34.7 days (Hilderbrand et al. 1996) to determine the turnover rate for whole blood samples for wolves. I freeze-dried whole blood samples and ground them into a powder using a ball grinder. Sub-samples of one or more hairs or a powdered blood sample of approximately 0.5 mg were placed into 5 x 3.5 mm tin capsules and loaded into a ThermoFinnigan Delta Plus Advantage continuous-

flow isotope ratio mass spectrometer at the Stable Isotope Ratio Mass Spectrometry and C/N Elemental Analysis Laboratory, University of Alberta, Edmonton, Alberta. Isotope signatures were expressed in delta notation as ratios relative to Pee Dee Belemnite (carbon) and atmospheric N_2 (Air) standards. Variation among repeated measures of sub-samples of hairs from within the same sample was ±0.22‰ for $\delta^{13}C$ and ±0.67‰ for $\delta^{15}N$, based on blind replicates (n = 22). Analytical machine error was ±0.2‰ for $\delta^{13}C$ and $\delta^{15}N$.

3.2. Diet composition

I used a multiple-source mixing model (Isosource; U.S. Environmental Protection Agency, Corvalis, Oregon) to determine the relative range in proportions of four most-likely prey items in the diet of wolves. A unique solution cannot be found when there are many sources in a model, therefore Isosource uses an iterative approach to find all feasible solutions of source contributions that satisfy the isotopic mass balance (Phillips and Gregg 2003). In Isosource, I entered the isotopic end-point from prey sources, and selected a source increment of 1%, and a mass balance tolerance of ±0.1‰ (Phillips and Gregg 2003; Urton and Hobson 2005). I defined the isotopic end-points as the mean isotopic values derived from hair and blood samples after appropriate fractionation values were applied (Hobson et al. 2000; Urton and Hobson 2005). Mixtures often fall outside the mixing polygon because of individual variation in diet (G. Mowat, pers. comm.), so I adjusted any isotopic signature to the nearest likely solution that fell within the mixing polygon. I reported the 1st and 99th percentile from the Isosource output. The 1st percentile of the data is interpreted

as a point on a scale below which 1% of the distribution lies. Reporting reduced percentiles (e.g. 10^{th} and 90^{th}) may be more appropriate for management interpretation, but it reduces the certainty that the reported range contains the real solution because the underlying distribution of solutions is unknown (D. Phillips pers. comm.).

When the multiple-source mixing model (Isosource) reduced the model to two or three prey sources, I was able to refine the diet estimates by using a linear mixing model (IsoError 1.04: U.S. Environmental Protection Agency, Corvalis, Oregon; Phillips and Gregg 2001). Linear mixing models are used to partition two sources with a single isotopic signature ($\delta^{15}N$), or three sources with an additional isotopic signature ($\delta^{13}C$; Phillips and Gregg 2001). I further simplified the diet models by deleting prey sources of least interest that were also uncommon in the diet. First, I deleted any prey source that had a mean contribution of <5%, 1^{st} percentile equal to zero, and 99^{th} percentile <10%, (G. Mowat, pers. comm.) and reran the simplified model. Since mountain caribou was the species of interest, I developed a more conservative requirement for deletion for this species. After running the simplified model, I retained mountain caribou if it still had a mean contribution of <2.5%, 1^{st} percentile equal to zero, and 99^{th} percentile <5%. I reported the mean and 95% confidence interval (CI) for each source proportion from the IsoError output.

I corrected isotopic signatures for each prey source to account for differential fractionation between digestion and assimilation (Phillips and Gregg 2003). Isotopic fractionation is the change in isotope ratios that occurs between

the consumers tissues or hair and its diet (Peterson and Fry 1987). This relationship is poorly known for most species, including wolves. Therefore, I had the choice to apply a fractionation value from a similar species, or a generalized fractionation value based on diet groupings (Robbins et al. 2005) or trophic levels (DeNiro and Epstein 1978, 1981; Minagawa and Wada 1984). Based on feeding experiments, DeNiro and Epstein (1978) found that the whole body $\delta^{13}C$ of a consumer was slightly more enriched than its diet by up to 2‰. The general pattern of trophic enrichment of 1 - 2‰ $\delta^{13}C$ has been verified by a number of studies of mammalian and avian food webs (see Kelly 2000 for review). Deniro and Epstein (1981) later documented an average of 3‰ enrichment in whole body $\delta^{15}N$ with each trophic level. This diet-consumer fractionation value was further refined to a 3 - 4‰ enrichment in $\delta^{15}N$ with each trophic level (see Kelly 2000 for review). Robbins et al. (2005) determined that the variation in protein quality across diet groupings was the mechanism behind $\delta^{15}N$ fractionation values using data from 21 species and five dietary groupings to determine that the $\delta^{15}N$ fractionation value for mammals consuming mammals was 4.0 ±0.2‰.

Researchers also use fractionation values specific to their species of interest when data exist. For example, Ben-David (1996) used feeding trials on captive mink to elucidate fractionation values required for the interpretation of isotope work on martens (Ben-David et al. 1997), and mink (Ben-David et al. 1997). Roth and Hobson (2000) were the first to document the diet-consumer fractionation values for a terrestrial mammalian carnivore, using red foxes (*Vulpes vulpes*). These fractionation values (Roth and Hobson 2000) have been

used for wolf stable isotope dietary reconstruction (Urton and Hobson 2005; B. Milankovic, pers. comm.). However, Robbins et al. (2005) warn that the use of discrimination values determined from commercial diets may not be appropriate for wild animals that consume complex mixtures of foods within distinct, isolated foraging bouts.

Fractionation values are based on feeding trials where the difference in $\delta^{13}C$ and $\delta^{15}N$ are compared between the diet and the tissues, blood components or hair of the consumer. Measurements of hair versus other tissues is enriched in carbon by 1 – 2‰ in consumers (Ben-David et al. 2004), therefore a hair enrichment factor of -1.5‰ is applied to all consumer hair signatures if the fractionation value is based on other tissue measurements (Mowat and Heard 2006).

I initially applied the generalized fractionation values of +2‰ for carbon (Ben-David et al. 2004) and +4‰ for nitrogen (Robbins et. al. 2005) to the prey isotope values, and corrected $\delta^{13}C$ for hair enrichment (-1.5‰, Mowat and Heard 2006), but the resultant model was not plausible. Therefore, I applied a more species-specific isotope diet-hair fractionation value of +2.6‰ for carbon and +3.4‰ for nitrogen to the prey source isotopic signatures with no additional hair enrichment factor, based on red fox values (Roth and Hobson 2000). For whole blood samples, I used a diet-blood fractionation value for blood fractions (serum and cells) of +0.5‰ for carbon and +2.6‰ for nitrogen (Roth and Hobson 2000). The differences in fractionation values between blood and hair should take into account differences in internal physiological processes between the two types of

samples, therefore allowing for comparisons between tissue types. I did not apply a hair enrichment value to the $\delta^{13}C$ signature because Roth and Hobson (2000) provide fractionation values specific to hair, blood fractions, liver and muscle.

I assumed that there were no differences between neonate and maternal prey isotopic signatures. While differences may vary by species, environment and diet composition, moose calves do not differ in $\delta^{13}C$ and $\delta^{15}N$ signatures from their mothers (Jenkins et al. 2001). Neonate and maternal caribou isotope signatures differ by 1.9±0.1‰ for $\delta^{15}N$ during the first 70 days, and decrease to 0.6±0.1‰ 98 days after birth (Jenkins et al. 2001). Caribou $\delta^{13}C$ signatures do not differ during first three months after lactation (Jenkins et al. 2001). If differences in offspring and maternal isotope signatures occur, the general pattern is one of depleted ^{13}C and enriched ^{15}N in calves relative to adult females (Sare et al. 2005; Pilgrim 2007).

Dual-isotope mixing models assume that isotopic signatures of sources are significantly different from each other to reduce uncertainty in estimates (Phillips and Gregg 2001). Sources can be combined if they are not significantly different or if the grouping is logical and aids in interpretation (Phillips et al. 2005). I tested this assumption using the K nearest-neighbour randomization test with p-values corrected for multiple comparisons using a Bonferroni correction factor (Rosing et al. 1998). Prey species with very small sample sizes were aggregated based on visual clustering along isotopic compositional axes.

3.3. Statistical analysis

I used Levene's test to evaluate whether the variance of the percent caribou in wolf diet differed across wolf packs (Stata 2003). I also tested if the percent caribou within wolf diet (determined by stable isotope analysis) was related to caribou density within home ranges of five wolf packs, using Kendall's rank correlation coefficient τ. To do this, I calculated wolf pack home ranges using a 90% adaptive kernel with a h_{ref} smoothing parameter using all wolf VHF and GPS data from 2003 – 2006 (Borger et al. 2006). I used volume contouring as the most biologically relevant contour. I overlaid wolf pack home ranges with the corresponding caribou census year to determine the number of caribou within each wolf pack home range. Caribou censuses were completed in the study area in March 2004 and 2006 (Figure 3-2; Hooge et al. 2004; McLellan et al. 2006; Furk 2006). I calculated the density of caribou within each wolf pack home range by dividing the home range area (km^2) by the number of caribou within the corresponding home range. I used The Home Range Tools for ArcGIS (Version 1.1c, Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada) and ARCMAP 9.1 (Environmental Systems Research Institute, Redlands, CA, USA) for all GIS and home range analysis.

3.4. Extrapolating stable isotope relative proportions

Density of moose within the Goldstream and Downie wolf pack home ranges were determined from moose census data from Poole and Serrouya (Figure 3-2; 2003). Complete moose census data were only available for these two wolf

packs. I averaged the moose density for each wolf pack to obtain an average moose density for the study area. I used this density to determine the corresponding kill rate from Messier's (1994) functional response curve, adjusted to reflect five months of hair growth (moose/wolf/150days). I adjusted the winter kill rate (0.71; Messier 1994) to reflect summer kill rates corresponding to the time frame of the stable isotope analysis. To estimate the biomass of moose, I adjusted the summer kill rate by the mass of a moose (unknown sex = 400 kg; Hayes et al. 2000), the percent of the carcass that is edible (75%; Peterson 1977), and the percent of consumable biomass (75%; Hebblewhite 2000). I then multiplied the final moose biomass by the average pack size (kg moose/wolf pack/150 days). This approximates the actual consumption rate of moose by wolf packs; a measure comparable to the results of the stable isotope dietary results of assimilated biomass of average wolf packs. I calculated the number of caribou in the diet of wolf packs using the cross-product of the relative proportion of moose and caribou predicted by the isotope mixing model with the predicted biomass of moose eaten by wolf packs from the literature. I then back-corrected the resulting biomass to reflect the mass of an adult caribou (152 kg; Hayes et al. 2000) and calculated the number of caribou consumed/wolf pack/150 days.

4. Results

4.1. Sample collection

I collected hair samples from 18 caribou, 18 moose, three deer and one beaver, and from five wolf packs, including the Goldstream (8 samples), Park (3),

Mica (7), Jordan (2), and Downie (3). The majority of prey hair samples were collected from January – March, representing the previous year's spring to fall diet for each prey species. This may vary depending on the species individual molting pattern. I did not include samples from the Downie wolf pack in the analysis due to poor hair quality. I collected blood samples from the Goldstream (2 samples), Mica (2), Downie (2) and Jordan (2) wolf packs.

4.2. Isotopic signatures

Mean stable isotope values (± SE) for wolves in the north Columbia Mountains ($n = 20$) were -23.2 ± 0.1‰ for $\delta^{13}C$ and 5.9 ± 0.2‰ for $\delta^{15}N$, indicating little variation among individual wolves (Figure 3-3). When analyzed by wolf pack, the average stable isotope value was -23.3 $\delta^{13}C$ ± 0.20‰ for $\delta^{13}C$ and 6.1 ± 0.3‰δ for ^{15}N, indicating that variation between wolf packs was also small (Table 3-2; Figure 3-4). Mean hair $\delta^{13}C$ and $\delta^{15}N$ values differed among wolf packs (Table 3-2; Figure 3-4). Late winter stable isotope values for wolf packs ($n = 4$) were enriched in $\delta^{15}N$ and reduced in $\delta^{13}C$ compared to other seasonal isotope values (Table 3-5). Late spring ($n = 3$), late fall ($n = 2$), and mean year ($n = 3$) wolf pack isotope values were not distinct due to overlapping standard deviations, but late fall was enriched in $\delta^{13}C$ (Figure 3-5). Potential prey source isotope signatures were isotopically distinct from each other ($p < 0.05$) based on K nearest-neighbour tests and visual inspection (Table 3-1).

4.3. Diet composition

I determined the average wolf pack diet for late spring – late fall using hair samples from 28 wolves. The mixing polygon for the average wolf pack was broad and the mixture fell near one end of the polygon (Figure 3-6). This signified that the ranges of possible contributions from each source (potential prey) were constrained and informative (Phillips and Gregg 2003). Wolf packs (n = 4) relied significantly on moose (range: 91 - 99%, mean: 95.4%), followed by deer (0 - 8%, 2.6%), caribou (0 - 4%, 1.3%) and beaver (0 - 3%, 0.7%; Figure 3-6). I deleted beaver and deer from the model and used a single-isotope linear mixing model to refine diet estimates. I found that the proportion of moose and caribou in the diet of wolf packs was 97.1 ± 28.4% and 2.8 ± 28.4% respectively.

I adjusted three wolf pack stable isotope values to fall within the mixing polygon, but corrections were within one or two standard deviations and within sample variation. The Jordan, Park and Mica wolf packs had on average 32%, 5% and 2% more caribou in their diet than the Goldstream wolf pack. (Table 3-3). The Goldstream wolf pack reduced down to two prey sources, therefore the refined diet estimate was 98.7 ± 26.6% moose, followed by 1.2 ± 26.6% deer (Table 3-4). After the deletion of beaver and deer from the Park wolf pack diet model (Table 3-3), the proportion of caribou and moose was 5.0 ± 19% and 94.9 ± 19% respectively (Table 3-4). I removed beaver from the Mica wolf pack model (Table 3-3), leaving moose (78 ± 52.0%), deer (20 ± 42.8%) and caribou (2.2 ± 22.0%; Table 3-4) as major prey sources. I removed beaver and deer from the Jordon wolf pack diet model (Table 3-3). The refined model found that the

proportion of moose and caribou in the diet of the Jordon wolf pack was 68.2 ± 16.8% and 31.7 ± 16.8%, respectively (Table 3-4).

In the late fall, the proportion of caribou in the diet of wolves increased by 22%, compared to a total reliance on moose in the late spring (Table 3-5; Figure 3-7a). Wolves consumed a greater diversity of prey sources in the late winter (Table 3-5, Figure 3-7b), however the ranges were too broad to give meaningful information about partitioning among many of the prey sources (Figure 3-7a; Phillips and Gregg 2003). I did not simplify the late winter model because prey sources did not meet guidelines for deletion (mean > 5%, 1st percentile = 0, 99th percentile greater than 10%).

4.4. Statistical analysis

The variance in the percent of caribou in the diet of wolves (from stable isotope analysis) was not equal across wolf packs (Levene's test, $F_{(3,16)} = 6.03$, $p = 0.005$), and was not explained by density of caribou within each wolf packs home range, $\tau = -0.067$, $n = 6$, $p = 1.0$ (Table 3-6).

4.5. Extrapolating isotope relative proportions

Wolf packs within the north Columbia mountains ($n = 2$) had an average moose density of 0.52 moose/km^2 within their home ranges, resulting in an estimated winter kill rate of 1.75 moose/wolf/100days, based on Messier (1994). The corresponding wolf density at this moose density was estimated as 22.35 wolves/1000 km^2 (Messier 1994). After appropriate corrections were made, an average wolf pack killed 6.02 moose/pack/150days and 0.46

caribou/pack/150days during the five month period reflected by hair growth (late spring – late fall). This corresponded to an average relative proportion of 97.1% moose and 2.8% caribou in the average diet of a wolf pack based on stable isotope analysis. Individual wolves ate 0.91 moose/wolf/150days and 0.07 caribou/wolf/150days. Therefore, during the duration of the study, all five wolf packs ate approximately 1.9 caribou and 24.1 moose during the late spring to late fall, assuming that wolf packs had equal access to the same prey types and densities across the study area.

5. Discussion

I measured stable carbon and nitrogen isotope ratios in the hair and whole blood of grey wolves in the North Columbia Mountains, British Columbia to determine the relative importance of caribou and moose in the diet of wolves.

5.1. Average wolf pack diet

Moose comprised the majority of the average diet of wolf packs (95%), followed by small proportions of caribou, deer and beaver late spring – late fall. These results generally reflect the densities of prey species on the landscape, with moose as the most abundant prey species (0.71 – 3.56 moose/km^2; Poole and Serrouya 2003), followed by low densities of caribou (0.035 - 0.05 caribou/km^2), deer (est. 0.02 – 0.03 deer/km^2; R. Serrouya, pers. comm.) and beaver (density unknown). Thus, the predation patterns of wolf packs may be consistent with positive frequency-dependent predation, where predators concentrate on common prey items (Whelan et al. 2003). My results did not support the hypothesis that

negative frequency-dependent predation occurred. Higher relative proportions of caribou, deer and beaver would be expected to support this model. In fact, my analysis showed that the relative proportion of caribou within the diet of wolf packs was not related to caribou density. Wolf predation may be independent of caribou density because of spatial or temporal refuges (e.g. spatial separation; Forrester and Steele 2004), encounter rates occurring at random because of low caribou densities, and/or wolves focusing on abundant prey.

Previous diet reconstructions, based on scat analysis, found that moose comprised 47.7% of the summer biomass in the diet of wolves in the study area from 1993 – 1995 (Allison 1998). Beaver and caribou comprised 21.8% and 18.9% of the summer biomass respectively (Allison 1998). In an adjacent area, Seip (1992) found that between 1984 -1989, wolves were a major predator of caribou (20% of diet from scat analysis) in the summer in Wells Gray Park, B.C. Differences between the isotope and scat analysis results may be due to sampling bias, interpretation differences between methods, or the effects of changing predator-prey dynamics over time. Scat analysis may be biased by small sample sizes, collected mainly in lower elevations (e.g. Allison 1998), or problems with misidentification of moose and caribou hair (B. Harrower pers. comm.). Results are also difficult to compare between methods, because stable isotope analysis estimates relative assimilated biomass while scat analysis estimates percent occurrence or biomass in feces. The landscape has also changed since studies completed by Seip (1992) and Allison (1998). There has been an increase in the amount of early seral stage forest, due to forest harvesting, that in turn may

support higher prey and predator densities. For example, moose densities have more than doubled in the north Columbia Mountains in the past decade (Poole and Serrouya 2003).

Beaver, found to constitute an important summer food source for wolves in most areas (e.g. Peterson and Ciucci 2003), were not an important food source in the north Columbia Mountains during this study. The amount of riparian habitat available for beavers may be limited because of steep, narrow valleys, fast flowing rivers and flooding from reservoir creation. Consequently, beaver may remain a relatively limited food source for wolves in the future.

Predators such as wolves, grizzly bears, and wolverine feed seasonally on newborn ungulates (Gustine et al. 2006). If signatures of neonate and maternal prey species are significantly different, then researchers may be able to detect the proportion of neonate prey to adult prey in the diet of predators. Caribou offspring isotope signatures differ from their mothers within the first 70 days (Jenkins et al. 2001), but I did not incorporate potential differences into my analyses of wolf diet. As a result, my models may overestimate the contribution of caribou to the diet of wolves, because caribou isotopic signature may be a mixture of both neonate and maternal sources (see Jenkins et al. 2001).

5.2. Wolf pack variation in diet

At the broad scale, differences between wolf pack diets may be explained by differences in home range characteristics that shape the prey composition and density at smaller scales. The Jordan wolf pack had a higher relative proportion of caribou in their diet compared to other wolf packs. The Goldstream, Park and

Mica wolf packs home ranges were within the Northern Kootenay Mountain ecosection, while the majority of the Jordan wolf pack home range extended into the Shuswap Highland ecosection to the west (Figure 3-1; Demarchi 1996). The Shuswap Highland ecosection is characterized by rolling highland topography compared to the rugged, ice-capped mountainous terrain of the Northern Kootenay Mountain ecosection (Demarchi 1996). The less rugged landscape of the Shuswap Highland ecosection may reduce the ability of caribou to spatially separate themselves (e.g. Bergerud et al. 1983; Bergerud and Page 1987; Seip 1992; Cumming et al. 1996; James et al. 2004), resulting in higher predation rates by wolf packs. Levels and patterns of forest harvesting and road building may also differ between ecosections, possibly affecting local predator-prey dynamics. Large confidence intervals bounding each diet estimate indicate that increases in sample sizes are required to increase the reliability of the estimates.

At finer scales, wolf pack diets may be influenced by local densities of prey species. The Goldstream wolf pack had the highest moose densities within the core of their home range, reflected in the high relative proportion of moose in their diet. The Mica and Park wolf packs had medium to low moose densities, and consequently lower relative proportions of moose in their diet. There were no moose density estimates for the Jordan wolf pack, but a recent moose census to the north (Caribou Mountains ecosection) indicates substantially less moose than the Northern Kootenay Mountains ecosection (Serrouya and Poole 2007). Lower moose densities within wolf pack home ranges may have resulted in higher relative proportions of secondary prey sources (deer, caribou, beaver) in the diet.

Increased sample sizes and corresponding prey densities for each wolf pack home range are needed to confirm whether these differences are consistent, and what factors best explain the variation in the diet of wolf packs.

5.3. Seasonal variation

There was an apparent seasonal shift in the late fall and late winter diets of wolf packs. However, these results should be interpreted with caution as there were a number of biological, sampling, and modeling factors that could have contributed to this result. Prey diet may change significantly with seasons (e.g. caribou dependence on lichen in late winter compared to spring) and this may be reflected in a change in the prey isotopic signature for that season. Ideally, prey samples should be collected throughout the year to determine if changes in diet are evident in isotope signatures before attempting seasonal diet reconstructions. I also used isotopic fractionation values for blood serum and cells and not whole blood, therefore the isotopic fractionation value used in the late winter for blood may vary from the previously published result (Roth and Hobson 2000). The general patterns I documented are nevertheless of interest in advancing understanding and guiding future sampling efforts.

In the late fall, average wolf pack diet showed increased relative proportions of caribou, and decreased relative proportions of moose. Seip (1992) also found wolf predation on caribou varied seasonally, with the majority occurring during summer and early winter. When all predator-caused caribou mortalities in B.C. are combined by season, the calving and summer seasons have the highest number of mountain caribou mortalities per day (Wittmer et al. 2005).

The late winter diet model produced results that were inconclusive, because the broad ranges of feasible prey contributions produced by the models. This occurred because the average wolf pack isotope signature fell near the center of the mixing polygon (Phillips and Gregg 2003). Therefore, the diet was composed of approximately equal mixtures of food sources (Phillips and Gregg 2003). For example, ranges were large because there was approximately equal mixtures of moose and beaver, or caribou and deer plus some contribution of beaver. Interpreting these ranges requires tradeoffs among the food contributions so that the probable diet is equal to 100%. Phillips and Gregg (2003) use the example that if one source has the maximum feasible contribution, then some of the other food sources must have contributions closer to the lower end of their range. Alternatively, I could use information on the distribution and densities of prey to discount certain diet options (Phillips and Gregg 2003). In my study system, deer and caribou densities are very low and incapable of sustaining wolf packs, and the separation of caribou and wolves is greatest in the late winter. Therefore, a late winter diet composed of mainly moose and beaver is plausible. Overall, the general pattern in the late winter was that the relative proportion of moose declined, beaver and deer increased, and caribou results were inconclusive.

Seasonal variation in the diet of wolves may reflect the level of spatial separation experienced by caribou and wolves. The spatial separation between caribou and wolves was high in the late winter (Jan. 16 – March 31), low during spring (April 1 – May 23) and calving (May 24 – June 15) and moderate in the summer (June 16 – Oct. 22) and early winter (Oct. 23 – Jan 15; Chap. 2). The

stable isotope seasons, created from splitting hairs in half, approximate the calving (late spring), summer (late fall) and late winter (late winter) seasonal designations of caribou (date of greatest elevational change; Apps et al. 2001) used in Chapter 2. The relative proportion of caribou increased in the late spring (0%) to the late fall (22%), however this does not coincide with the increasing degree of spatial separation in these seasons. I expected that the relative proportion of caribou would be highest in seasons that had the lowest levels of spatial separation. Late winter is when caribou have the highest spatial separation from wolves (Chap. 2), however the stable isotope diet proportions were inconclusive for this season.

5.4. Extrapolating isotope relative proportions

Stable isotope diet reconstruction provides the relative proportions of prey sources in the diet of wolves but not actual numbers. The relationship between moose density and wolf kill rate is well documented in the literature (Messier 1994), thus it is feasible to estimate actual numbers from stable isotope data. This information was valuable to describe summer predation patterns of wolves and quantify the potential impact of wolf predation on moose and caribou. However, this analysis was based on adult biomass estimates, and studies show that newborn ungulates in spring and summer constitute much of summer wolf diet (Jedrzejewski et al. 2002; Mech and Peterson 2003, Gustine et al. 2006). The accuracy of the estimates would be improved if the ratio of adult to calf mortality due to wolves was known.

Three out of four wolf packs showed small relative proportions of caribou in their diet, suggesting that at least one caribou was eaten in each of these three wolf packs. However, two out of three wolf packs had diet estimates with confidence intervals overlapping zero. Therefore, the estimate of two caribou eaten by five wolf packs between late spring – late summer may be a realistic approximation.

5.5. Other considerations

Stable isotope analysis has many benefits over traditional diet analysis, but as the use of this technique expands to address new topics and applied to new species, further research regarding the impact of ^{13}C fractionation values, individual sample variation, nutritional ecology, variation in hair growth, and factors affecting carbon and nitrogen isotopes would reduce uncertainty in isotope proportions (Hobson et al. 2000; Phillips and Gregg 2001; Robbins et al. 2005; Jones et al. 2006). For instance, ^{15}N signatures can be increased by predation on neonates (Hobson and Sease 1998), nutritional stress (Hobson and Clark 1992), or trophic level of prey species (Deniro and Epstein 1981; Minagawa and Wada 1984). There was no evidence that these factors biased ^{15}N signatures in my analysis, although neonates are an important summer prey source for wolves (Adams et al. 1995; Gustine et al. 2006). Elevated ^{15}N signatures would have resulted in higher relative proportions of deer, caribou and beaver in the diet of wolf packs, but results showed that wolf pack signatures were centered around the moose signature in most cases. The late winter wolf pack signature had an elevated ^{15}N signature, but neither the consumption of neonates or nutritional

stress were factors in this season. The stable nitrogen isotope fractionation value applied to prey sources may be slightly elevated because red foxes were fed a commercial diet (50% carbohydrate) that differed from their wild diet consisting mainly of protein and fat from animal tissues (Roth and Hobson 2000). Controlled studies that attempt to replicate the diet of wild animals when determining fractionation values would improve the accuracy of diet estimates for wild animals (Robbins et al. 2005).

The power of this study could be increased by acquiring more samples, expanding analysis into the early winter, and improving error estimates on samples. Several hairs from the same individual as well as duplicates of each sample should be run to investigate the influence of sample variance and machine error on the estimates (Ben-David et al. 2004; Mowat and Heard 2006). Increasing the number of paired samples (base and tip of hairs) would strengthen the analysis of seasonal variability in wolf pack diet.

6. Conclusions

I found that moose were the main prey source of wolf packs in the north Columbia Mountains based on stable isotope diet reconstruction. These results were consistent with other systems where moose is the main prey source for wolves when elk or deer are lacking (Peterson and Ciucci 2003). Caribou made up a relatively small proportion of wolf diet, but results suggested that this relative proportion increased in the late fall. The average diet of wolf packs suggested a pattern consistent with positive frequency-dependent predation.

There have been significant changes in species composition and abundance in the north Columbia Mountains. The coexistence of moose and caribou is a recent event in central and southern British Columbia, after a significant natural range expansion of moose in the 1900's (Tefler 1984; Karns 1998; Kelsall and Telfer 1974), and a more recent doubling of moose densities in the last decade within the study area (Poole and Serrouya 2003). Based on theoretical models (Holt 1977; Holt and Kotler 1987; Holt and Lawton 1994; Courchamp et al. 2000) and work on invasive species (Smith and Quin 1996), my data suggested that apparent competition may be occurring between moose, wolves and caribou. However, my analysis illustrated that the relative proportion and total number of caribou in the late spring – late fall diet of wolf packs was small. This leaves two important questions for researchers; 1) what proportion of caribou in wolf pack diets is necessary to exacerbate caribou population declines, and 2) can caribou populations withstand random predation events by wolves? In the case of hyperpredation (a more restricted version of apparent competition specific to island ecosystems), high levels of predation are not required, but "higher than normal" levels result in the extinction of the secondary prey source (Courchamp et al. 2000). The secondary prey source may escape extinction if it has a high intrinsic growth rates and/or carrying capacity as well as anti-predator strategies effective with the predator (Courchamp et al. 2000). The antipredator strategy of caribou (spatial separation) may be effective at delaying or halting population declines if survival of neonates is high.

Wildlife management strategies, aimed at increasing caribou survival, should target initiatives that will have the greatest impact on caribou recovery. In 2004, a scientific panel made a number of management recommendations, including the liberalized hunting of predators and other ungulates (Messier et al. 2004). This panel did not recommend long-term wolf reduction without clear evidence that wolf predation is a primary cause of caribou population declines. Previous stable isotope analysis found that caribou was a probable food source in the late spring - late fall diets of wolverine and grizzly bears in the north Columbia Mountains (Stotyn et al. 2007), although scavenging and direct predation could not be separated. Wolverine had the highest relative proportion of caribou within their diet (10%; Stotyn et al. 2007), however these proportions represented diets from 1993 – 1999 when caribou numbers were approximately 43% higher than population estimates completed in 2006 (McLellan et al. 2006). Grizzly bears may be a source of caribou mortality, although the possible range of caribou within their diet was small (0 – 3%). Caribou did not appear in the assimilated diets of wolves or cougar. Therefore, it is difficult to conclude that wolves were a primary cause of caribou mortality during late spring to late fall 2003 - 2006. In addition, the steepest part of the caribou population decline occurred during 1997 – 2002 (McLellan et al. 2006). Current wolf pack diet reconstruction reflected current predation patterns on low, but stable caribou populations. Wolf pack diet during the steepest part of the decline phase of caribou (1997 – 2002) could have produced different results.

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Table 3-1. Summary of the means, standard deviations (SD) and ranges (min to max) for $\delta^{13}C$ and $\delta^{15}N$ values for hair of four potential prey species of wolves, sampled from the north Columbia Mountains, British Columbia from 2003-2005 (not corrected for consumer diet-hair fractionation).

Potential Prey Species	*n*	$\delta^{13}C$ (‰)	$SD^{13}C$	Range (‰)	$\delta^{15}N$ (‰)	$SD^{15}N$	Range (‰)
Beaver	1	-24.2	-	-	7.2	-	-
Caribou	18	-24.1	0.85	-25.9 to -22.3	5.0	1.06	2.8-6.4
Deer	5	-26.5	0.73	-27.2 to -25.5	4.5	1.55	3.0-7.0
Moose	18	-25.9	0.59	-26.8 to -25.0	2.6	0.88	1.0-4.8

Table 3-2. Summary of the means, standard deviations (SD) and ranges (min to max) for $\delta^{13}C$ and $\delta^{15}N$ values for hair of four wolf packs sampled from the north Columbia Mountains, British Columbia from 2003-2006.

Wolf Pack	*n*	$\delta^{13}C$ (‰)	$SD^{13}C$	Range (‰)	$\delta^{15}N$ (‰)	$SD^{15}N$	Range (‰)
Goldstream	8	-23.4	0.44	-23.8 to -22.6	5.3	0.35	4.9-5.9
Park	3	-23.0	0.65	-23.5 to -22.3	5.8	0.17	5.6-6.0
Mica	7	-23.4	0.48	-24.4 to -23.0	6.5	1.08	5.9-8.9
Jordan	2	-22.6	0.10	-22.7 to -22.5	6.4	0.13	6.3-6.5
Average*	4	-23.3	0.48	-23.4 to -22.6	6.1	0.44	5.3-6.4

* does not include Downie Pack

Table 3-3. Initial multi-source mixing model results (Isosource) for the relative contribution and standard deviation of prey items wolf pack diets in the north Columbia Mountains, British Columbia from 2003-2006.

Species	Goldstream (%)	SD	Park (%)	SD	Mica (%)	SD	Jordon (%)	SD
Beaver	0	-	0	-	0	-	0 - 2	0.8
Caribou	0	-	9	-	0 – 7	2.0	32 - 35	1.0
Deer	0 - 1	0.7	0	-	12 - 27	3.6	0 - 2	0.7
Moose	99 - 100	0.7	91	-	72 - 83	3.1	64 - 66	0.8

Table 3-4. Single-isotope and dual-isotope linear mixing model results (IsoError) for the percent and standard error of prey items wolf pack diets in the north Columbia Mountains, British Columbia from 2003-2006. Less common prey species were removed from the initial multi-source mixing model.

Species	Goldstream (%)	SE	Park (%)	SE	Mica (%)	SE	Jordon (%)	SE
Beaver	-	-	-	-	-	-	-	-
Caribou	-	-	5.0	9.0	2.1	10.6	31.7	7.7
Deer	1.2	12.8	-	-	20.0	20.3	-	-
Moose	98.7	12.8	94.9	9.0	77.7	23.6	68.2	7.7

Table 3-5. Relative contribution and standard deviation of prey items to wolf diets for four time periods in the north Columbia Mountains, British Columbia from 2003-2006. Seasonal samples were extracted from the base (late fall) and tip (late spring) of wolf guard hairs (from Darimont and Reimchen 2002), and blood collected in March representing a 70 day time frame from Jan. 4 – March 15 (late winter). The mean year is a whole guard hair representing the diet from late spring to late fall (4-5 mo.; Darimont and Remchen 2002).

Species	Late Spring [1] (%)	SD	Late Fall [2] (%)	SD	Late Winter [3] (%)	SD	Mean Year [4] (%)	SD
Beaver	0	-	0	-	20 - 50	7.6	0	-
Caribou	0	-	26 [5]	-	0 - 36	9.6	0	-
Deer	0	-	0	-	20 - 48	7.0	0	-
Moose	100	-	74 [6]	-	0 - 30	8.2	100	-

[1] Goldstream (n = 5), Park (n = 1), Jordan (n = 2)
[2] Goldstream (n = 3), Jordan (n = 2)
[3] Goldstream (n = 2), Downie (n = 2), Jordan (n = 2), Mica (n = 2)
[4] Goldstream (n = 3), Park (n = 2), Mica (n = 7)
[5] 22.2 ± 31.6% (95% CI) from single-isotope ($\delta^{15}N$) mixing model
[6] 77.7 ± 31.6% (95% CI) from single-isotope ($\delta^{15}N$) mixing model

Table 3-6. Information used to calculate the relationship between percent caribou in diet and caribou density within each wolf pack home range in the north Columbia Mountains, British Columbia between 2003 - 2006.

Wolf Pack	Mean Relative Percent of Caribou in Diet	Home Range Area (km^2)	Number of Caribou within Home Range	Caribou Density (caribou/km^2)	Estimated Wolf Pack Size [2]
Goldstream (2004)	0.0	1635.06	24	0.015	7.0
Goldstream (2006)	19.1	1369.23	31	0.023	5.0
Park [1]	5.0	2004.10	28	0.014	7.5
Jordan	31.7	6834.91	89	0.013	8.0
Mica	2.1	2710.02	33	0.012	5.0
Downie	0.70	2302.06	31	0.014	12.0

[1] home range of "Park" wolf pack was estimated using the average pack size from the literature (Fuller et al. 2003)

[2] wolf pack size estimated during late-winter captures

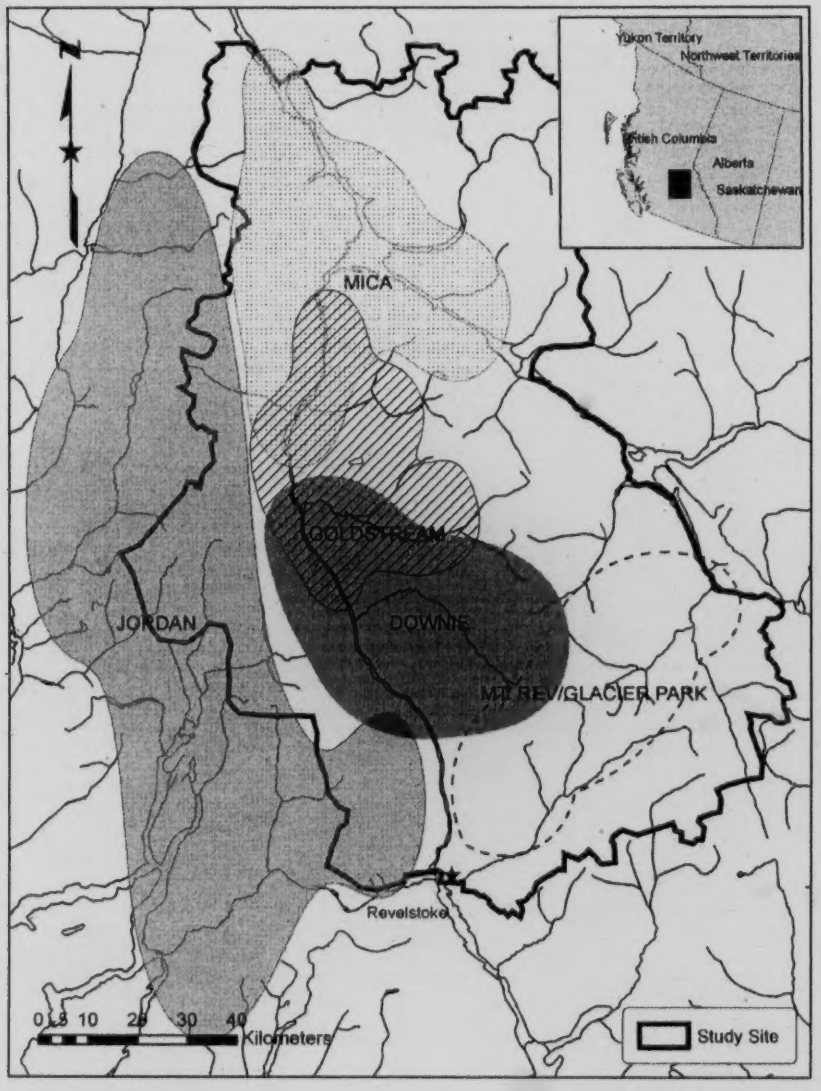

Figure 3-1. Outline of the study area encompassing the north Columbia Mountains, British Columbia. Included wolf home ranges (90% adaptive kernel volume) from VHF and GPS locations (2003-2006). The location of Mt. Revelstoke/Glacier Park home range was estimated (dashed line) for visual purposes only, because there were no collared individuals to accompany the stable isotope samples.

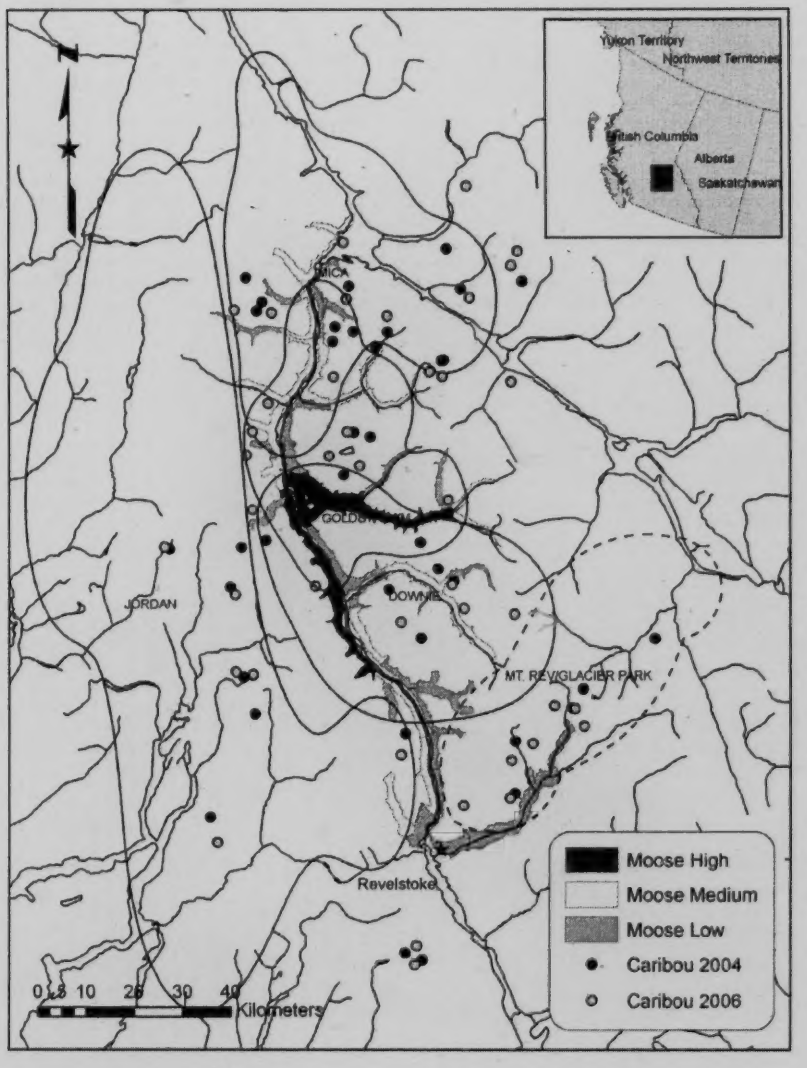

Figure 3-2. Mountain caribou (2004 & 2006) and moose census data (2003) overlaid with wolf pack home ranges (90% adaptive kernel volume) from wolf VHF and GPS locations (2003-2006). The location of Mt. Revelstoke/Glacier Park wolf home range was estimated (dashed line) for visual purposes only, because there were no collared individuals to accompany the stable isotope samples.

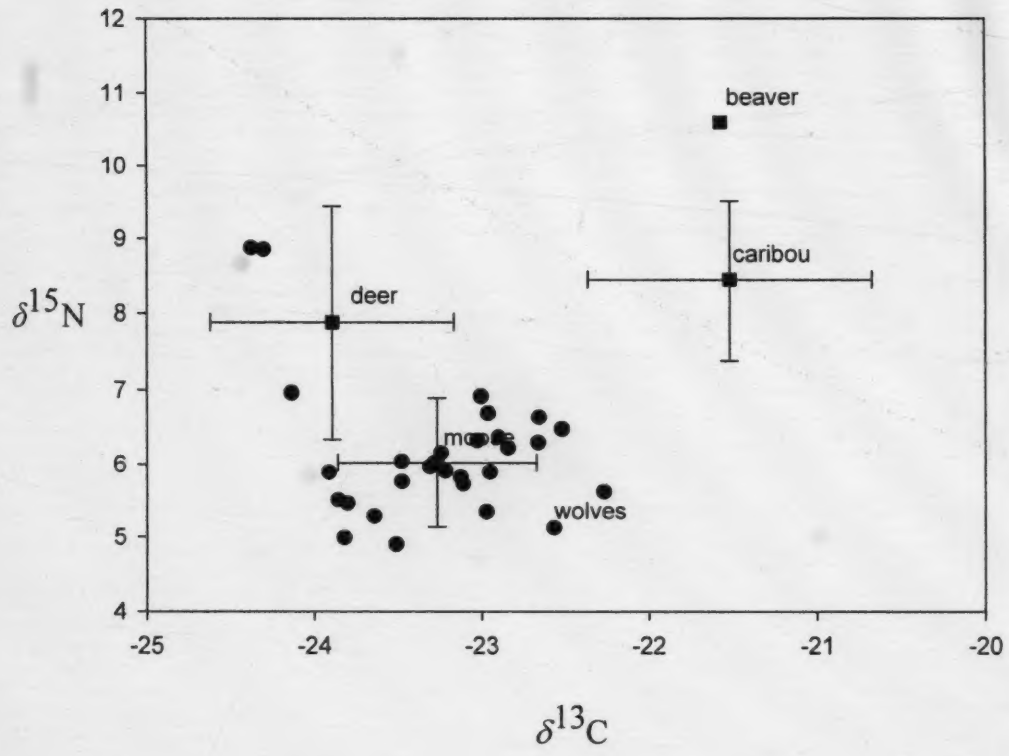

Figure 3-3. Distribution of mean δ^{13}C and δ^{15}N hair values (‰;±*SD*) for four main prey sources of wolves (■) and individual wolves (●). Wolves were sampled from five wolf packs in the north Columbia Mountains from 2003-2006. Prey sources were corrected for diet-hair fractionation (Roth and Hobson 2005).

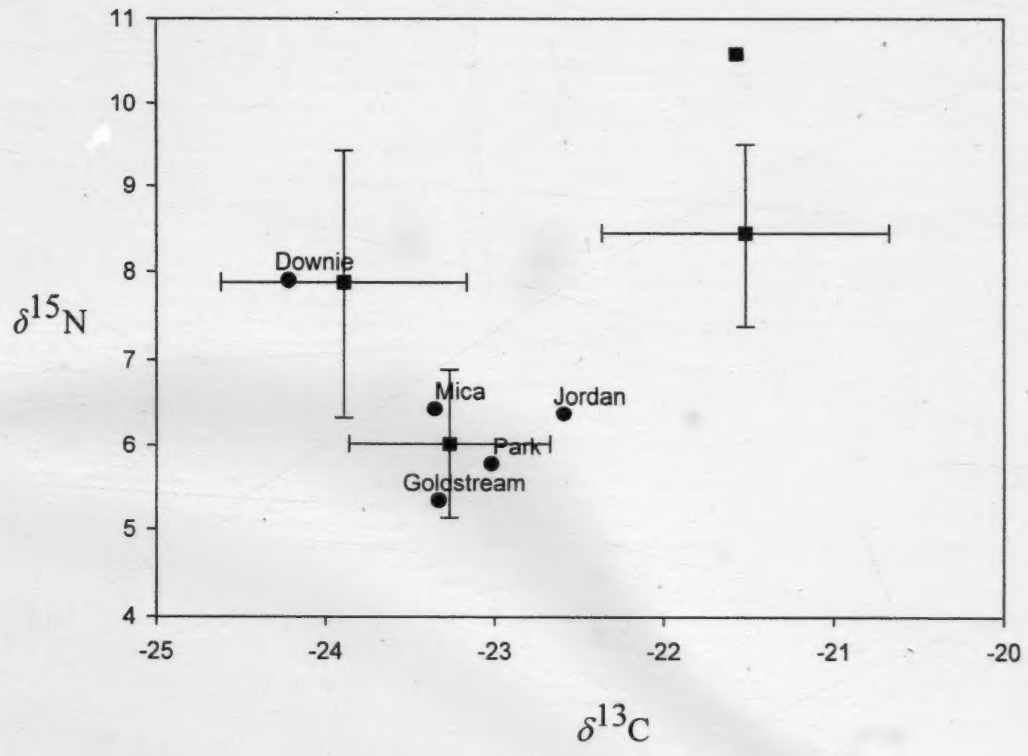

Figure 3-4. Distribution of mean $\delta^{13}C$ and $\delta^{15}N$ hair values (‰; ±SD) for four prey sources (■), and five wolf packs (●) and sampled in the north Columbia Mountains from 2003-2006. Prey sources were corrected for diet-hair fractionation (Roth and Hobson 2005).

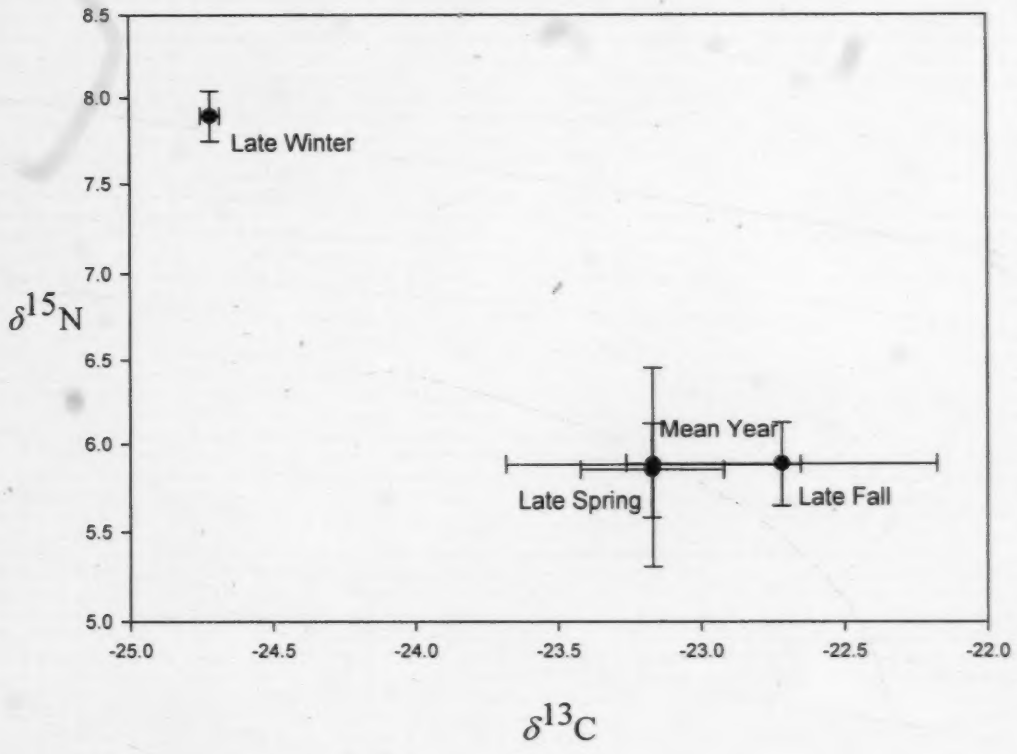

Figure 3-5. Mean values of $\delta^{13}C$ and $\delta^{15}N$ (± SD) for late spring ($n = 3$), late fall ($n = 2$), late winter ($n = 4$) and the year average ($n = 3$) for wolf packs sampled in the north Columbia Mountains from 2003-2006. Seasonal samples were extracted from the base (late fall) and tip (late spring) of wolf guard hairs (from Darimont and Reimchen 2002), and blood collected in March (late winter). The mean year is a whole guard hair collected in March that represented the diet from spring to fall.

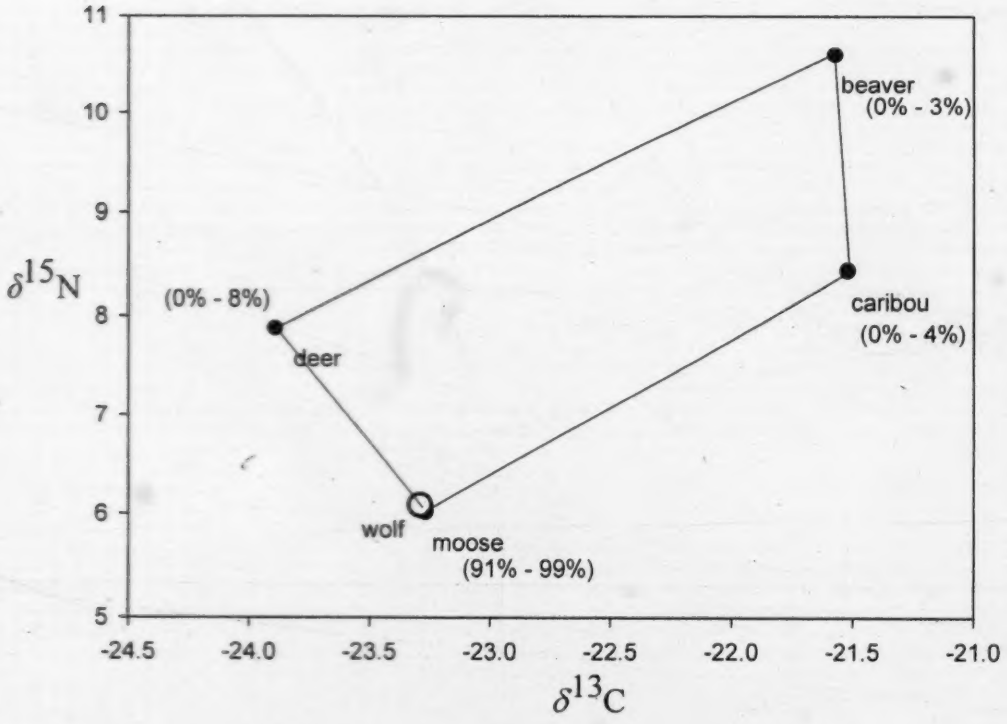

Figure 3-6. Isosource mixing polygon for the mean $\delta^{13}C$ and $\delta^{15}N$ hair values (‰) for four prey species of wolf packs ($n = 4$) in the north Columbia Mountains, British Columbia from 2003 - 2006. I reported the 1^{st}-99^{th} percentile ranges for the calculated feasible distributions in Isosource. Prey sources were corrected for diet-hair fractionation (Roth and Hobson 2005).

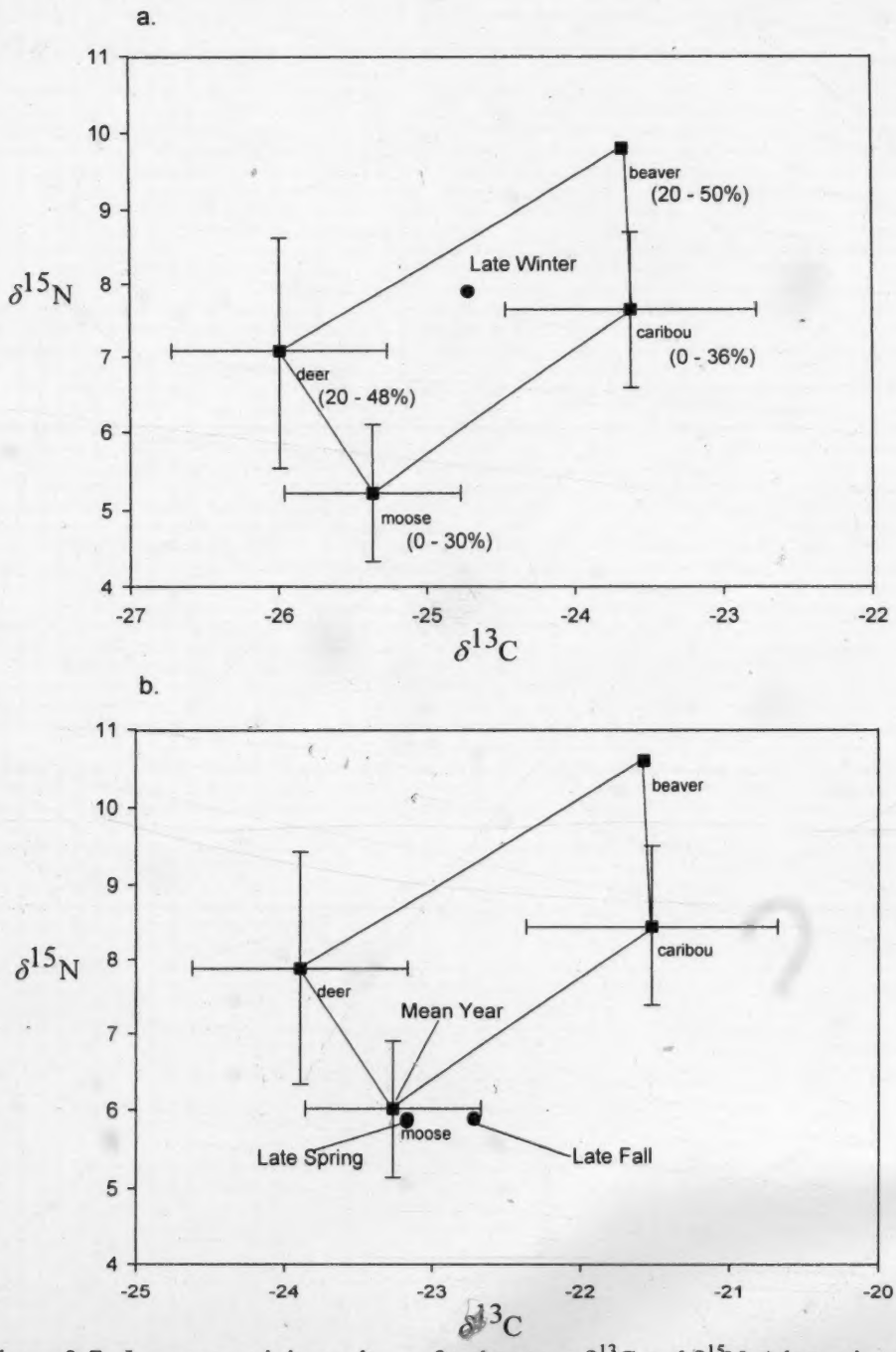

Figure 3-7. Isosource mixing polygon for the mean $\delta^{13}C$ and $\delta^{15}N$ a) late winter blood samples ($n = 4$), and b) mean year ($n = 3$), late spring ($n = 3$) and late fall ($n = 2$) hair samples for wolves in the north Columbia Mountains, British Columbia. The 1st-99th percentile ranges for the calculated feasible distributions are listed in Table 4. n represented the number of wolf packs sampled..

Chapter 4: Management Implications

Numerous documents have been produced on mountain caribou in British Columbia. These documents make recommendations for managers on the topics of ecosystem management (Seip 2000), access (Government of British Columbia 1999), forestry (Government of British Columbia 1999; Stevenson et al. 1999; Terry et al. 2000; Quesnel and Waters 2000; Johnson et al. 2004), habitat requirements (Simpson et al. 1997), and recovery options (Wildlife Branch 1997; Mountain Caribou Technical Advisory Committee 2002; Messier et al. 2004).

The most recent documents released by the BC Species at Risk Coordination Office (Mountain Caribou Science Team 2005) outlined four management options to recover mountain caribou in B.C. These recommendations include reducing predation, maintaining and improving habitat, reducing disturbance, and supplementing subpopulations. Predator management actions recommended by the Mountain Caribou Science team (2005) are aimed at reducing caribou mortalities. They suggest that predation can be reduced by managing predators directly, managing primary prey on which predators depend, and managing the habitat of primary prey (Mountain Caribou Science Team 2005). These strategies have been adopted in the North Kootenay Caribou Recovery Action Plan (Hamilton et al. 2003) for the Revelstoke, Central Rockies, Central Selkirk and Monashee subpopulations. The results of my analyses provide information to guide recommendations in the areas of reducing predation by wolves and managing habitat of primary prey.

1. Reducing predation

Current policies for the recovery of mountain caribou in B.C. suggest intensifying predator-prey management through management of access, predators and alternate prey species (Mountain Caribou Science Team 2005). Management would target individual predator species when there is evidence that supports that they are responsible for caribou mortalities (Mountain Caribou Science Team 2005). Does the data presented in my thesis provide compelling evidence that wolves should be a focus of predator management efforts in the north Columbia Mountains?

I used two techniques to examine the role of wolves in the decline of mountain caribou; mortality investigations and diet reconstruction via stable isotope analysis. Using data from a long-term mortality study (1992 – 2006), I found that wolves were not the primary predator of caribou before or after 2000, although the incidence of wolf predation increased after 2000. Stable isotope analysis indicated that wolf pack diets were dominated by moose (91 - 99%) with small relative proportions of caribou (0 – 4%), in the late spring – late fall (2003 – 2006). Stable isotope diet estimations coincided with seasons when the lowest degree of spatial separation between caribou and wolves was found (Chap 2). I also found that the relative proportions of caribou in the diet of wolf packs were not related to caribou density within each wolf pack home range. In summary, wolves were not the primary predator of caribou between 2003 – 2006 and based on this information should not be the focus of predator management efforts in the

north Columbia Mountains; however, density-independent predation may still have an impact on threatened populations of caribou.

What management techniques would be effective at reducing caribou predation if predation is largely based on the rate of encounter between wolves and caribou? If wolf functional response is dictated by time spent search and handling prey (Holling 1959), management efforts could target these components in three ways. Firstly, maintaining healthy moose populations would reduce search time and maximize handling time for wolves, therefore reducing encounter rates with caribou. However, moose populations would have to be maintained at a threshold level at which wolf populations were stabilized at medium-low densities. This option would be effective if combined with efforts to maintain the integrity of spatial refugia to preserve the spatial separation of moose, caribou and wolves. The introduction of spatial refugia in coral reef systems maintained density-independent predation (Forrester and Steele 2004). Secondly, managing the speed and efficiency by which wolves move on the landscape would reduce encounter rates. Movement rates and access into caribou habitat could be reduced by limiting road access in caribou habitat, regenerating old roads and reducing snowmobiling access into caribou habitat. Thirdly, reducing wolf populations would ultimately reduce encounter rates with caribou. Lessard et al. (2005), suggest a short-term wolf cull (10 year) in combination with a moose harvest policy as the most effective management strategy to recover caribou populations in Alberta, although these simulation models were applied to a boreal system where wolves are a major predator of caribou. This option may not be

appropriate or cost-effective in the north Columbia Mountains where wolves were not the primary predator of caribou between 2003 - 2006. If predator control measures were planned, an adaptive management approach (Walters 1986) should be undertaken using an experimental framework involving all major predators and monitoring population responses of moose, deer and caribou. Continued monitoring of caribou mortalities, and wolf diet through stable isotope analysis, should be implemented to monitor effects of management initiatives and mortality trends.

2. Managing habitat of primary prey

The Mountain Caribou Science Team (2005) states that predation can be reduced by creating habitat conditions that are unsuitable for deer, elk and moose. These recommendations include reducing the amount of shrub cover and other deciduous vegetation abundant in young forests, and maintaining large, contiguous patches of older forests (Mountain Caribou Science Team 2005).

While creating unsuitable habitat conditions for alternate prey, these management techniques may also maintain the integrity of spatial and temporal refuges for caribou. For example, my research showed that caribou consistently selected older forests (>140 yrs) more than wolves and moose in all seasons. Wittmer et al. (2007) found that caribou killed by predators have lower proportions of old forest and more mid-age forests in their home range when compared to live caribou. Therefore, these older forest age classes represent not

only a source of arboreal lichen for caribou, but a spatial refuge that minimizes predation risk from wolves. Non-forested areas including burns, slide paths, shrub areas and cutblocks were areas where there was similar use between caribou, moose and wolves in most seasons. Therefore, making these areas less attractive by reducing the amount of forage available for moose, may increase spatial separation and reduce predation risk in these habitats.

Caribou also selected Englemann spruce/subalpine fir forests and alpine areas relatively more than wolves and moose in most seasons. These forest types and areas may require special management when planning forestry, winter recreation and road building activities in mountain caribou habitat. Caribou used areas within 100 m of low-use roads relatively less when compared to wolves. Although these areas may pose a higher predation risk from wolves, more detailed analysis is required to disentangle the influence of elevation.

Analysis of resource selection does not provide mechanisms behind the patterns of resource use, but is useful for formulating hypotheses and encouraging future research. Future research priorities should explore the relationship between roads, caribou and wolves in more detail and experimental trials should monitor the response of caribou and moose to reductions in shrub cover in young forests.

Any management or recovery scenarios should focus on maintaining important variables contributing to spatial separation, particularly in the spring and calving seasons when the degree of spatial separation was lowest between caribou and wolves. Results identifying important factors contributing to spatial separation and the diet patterns of wolves can be used to guide management

decisions for mountain caribou recovery and serve as baselines with which to measure the effect of landscape change and habitat management efforts.

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